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A blue-green alga of carbonated mineral water

MARSHALL A. HOWE

(WITH PLATES 24 and 25)

Mr. Macey F. Deming of Tappan, New York, has directed the writer's attention to certain algae found on stones that have been piled up around the vent of a spring with geyser-like action at Saratoga Springs, New York, and apparently assisting in the deposition of crusts of calcium carbonate on such stones. Among these algae are species of *Microspora* and *Stichococcus* of the Chlorophyceae and a minute-celled member of the Myxophyceae (Cyanophyceae), the group more popularly known as the Blue-green Algae. The last-named is responsible for a striking blue-green or blue-purple coloration of the stones that attracts the attention of visitors. The spouting spring in question, according to information furnished by Mr. Herbert Ant, Senior Sanitary Chemist of the Saratoga Springs Commission, was formerly known as Pump Well No. 4, but was later renamed Polaris. The chemical composition of the water, he states, shows considerable variation from time to time. The water always contains large quantities of various soluble mineral salts, notably sodium chlorid, sodium bicarbonate, calcium bicarbonate, and magnesium bicarbonate. A rather recent analysis, made by Mr. Ant, is as follows:

Hypothetical combinations	
Ammonium chlorid	6.18*
Lithium chlorid	2.15
Potassium chlorid	154.02
Sodium chlorid	1,135.01
Potassium bromid	Trace
Potassium iodid	Trace
Sodium sulphate	Trace
Sodium metaborate	Trace
Sodium nitrate	Trace
Sodium nitrite	Trace
Sodium bicarbonate	741.14
Calcium bicarbonate	1,407.31
Barium bicarbonate	9.06
Strontium bicarbonate	Trace
Ferrous bicarbonate	10.51
Magnesium bicarbonate	461.93
Alumina	1.53
Silica	10.80
Total solids	3,939.64

* Milligrams per liter.

[THE BULLETIN FOR JUNE (60: 379–464) WAS ISSUED JUNE 1, 1933.]

Phormidium Demingii sp. nov.[1]

Forming thin (about 0.5 mm. thick) irregular cartilaginous, crustaceous, finally confluent, pulverulent-calcareous patches, externally aeruginous-olivaceous to blue-purple, internally prasinous, becoming minutely lacunose in older basal parts; filaments short (mostly 16–35μ long when well developed), erect-ascending, parallel or somewhat flexuous and intertangled, very closely compacted, giving surface, under the microscope, a very minutely cellular Oncobyrsoid appearance; trichomes 0.8–1.4μ in diameter; sheaths very soft and mucilaginous, wholly diffluent and invisible; cells (protoplasts) subquadrate, 0.7–1.6μ long, 1–1 1/2 times as long as broad, very distinctly segregated, separated by 1/4–1/2 their own length, apical cell rounded-obtuse; trichomes often dissolving into hormogonia of one or two cells which grow out in various directions, giving irregular or confused effects.

Forming a calcareous coating on stones that are kept continuously wet by the spray of the Polaris Spring, Saratoga Springs, New York, Macey F. Deming, October, 1932.

In its minute subquadrate cells and in its habitat, *Phormidium Demingii* may suggest *P. foveolarum* (Mont.) Gom. (type from roadside between Magny en Vezin and Mantes, France), but it differs amply in color, in the much shorter, less rigid, less moniliform, erect-ascending filaments, in the relatively longer and more widely spaced protoplasts, etc. The pulverulent calcification is perhaps not to be considered a diagnostic character, for considerable areas, microscopically speaking, show no lime. See also the observations of Frémy on *Rivularia dura* (Ann. Protistol. **3** (2/3): 69–79. 1931).

In its mostly erect-ascending filaments, *Phormidium Demingii* is slightly suggestive of *Oncobyrsa Cesatiana*, but, in spite of the frequent occurrence of solitary or geminate cells, the structure is essentially filamentous and not Chroococcaceous. In surface view, under the compound microscope, the structure may seem to be minutely cellular rather than filamentous, but that is because most of the filaments present their apices to the observer.

[1] Stratum externe aerugineo-olivaceum aut, in siccitate, caeruleo-purpureum, interne prasinum, tenue (ca. 0.5 mm. crassum), irregulare, cartilagineum, crustaceum, pulverulenti-calcareum. Fila brevia (plerumque 16–35μ longa, quum bene evoluta), erecti-ascendentia, subparallela aut plus minusve flexuosa et intricata, compacta, superficie strati minute cellulosa sub microscopia visa. Vaginae in mucum gelatinosum amorphum hyalinum diffluentes. Trichomata prasina, 0.8–1.4μ crassa. Cellulae (protoplasta) subquadratae, 0.7–1.6μ longae, 1–1 1/2-ies longiores quam latae, distincte segregatae, a 1/4–1/2 suae longitutudinis separatae, cellula apicali rotundati-obtusa. Hormogonia uni-aut bi-cellularia frequentes et, quoqueverse crescentia, facies confusas saepe fingentes. Planta stratum calcareum in lapidibus irroratis ad "Polaris Spring," in urbe Saratoga Springs, Novae-Eboracae, efficit. Legit Macey F. Deming, Oct. 1932.

One finds occasional larger ovoid cells, about 3μ in diameter, single or aggregated, with suggestions of division into smaller cells, but they occur chiefly in older, interior parts of the colonies and it is probable that they are intrusions of another organism—probably a member of the Chroococcaceae. There are rarely, however, conglobations of small cells that evidently belong to the species here described, but they may be fortuitous aggregations of cells floating in the mounting fluid rather than gonidia in a gonidangium. The minuteness of the cells and the absence of any visible cell walls make accurate observation difficult and erroneous inference easy. If sporangia or gonidangia are really present, the organism would seem to find its proper affinity in or near *Radaisia* of the Chamaesiphonaceae. However, there is no attachment of the filaments in the stages studied.

Associated with our plant are occasional more or less isolated filaments of the more conventional *Phormidium* type—longer, slightly broader, much more rigid, with obscure dissepiments and longer protoplasts—perhaps closely allied to *Phormidium tenue* (Menegh.) Gom.

The water of the Polaris Spring is, at the time of its discharge, supersaturated with carbon-dioxide gas.[2] Although intermittent, the discharges of the Polaris Spring are so frequent that the algae on the sprayed stones do not have an opportunity to dry out. As the water falls on the stones, the gas is released in the form of small bubbles (plate 24, fig. 2), so that the algae are continuously bathed in a fizzing highly mineralized water. It is probable that, whether carbonated or not, the waters in which the primordial algae lived were richer in mineral salts than those in which most of our so-called freshwater algae of the present day are found, so that the alga described above as new is of interest in the biologic as well as the systematic field.

THE NEW YORK BOTANICAL GARDEN

[2] The report of Dr. David H. Newland states that in some of these Saratoga springs "the waters contain as much as five or six volumes of carbon dioxide." N. Y. State Mus. Bull. Nos. **223, 224**: 159. 1921.

Explanation of plates 24 and 25

Plate 24

Fig. 1. Type locality of *Phormidium Demingii*, the crusts of which may be seen, especially on the larger lower stone at the right. The vent of the Polaris Spring, Saratoga Springs, N. Y. Photograph by M. F. Deming, October, 1932.

Fig. 2. Water from the Polaris Spring, showing release of carbon dioxide. Photograph by M. F. Deming.

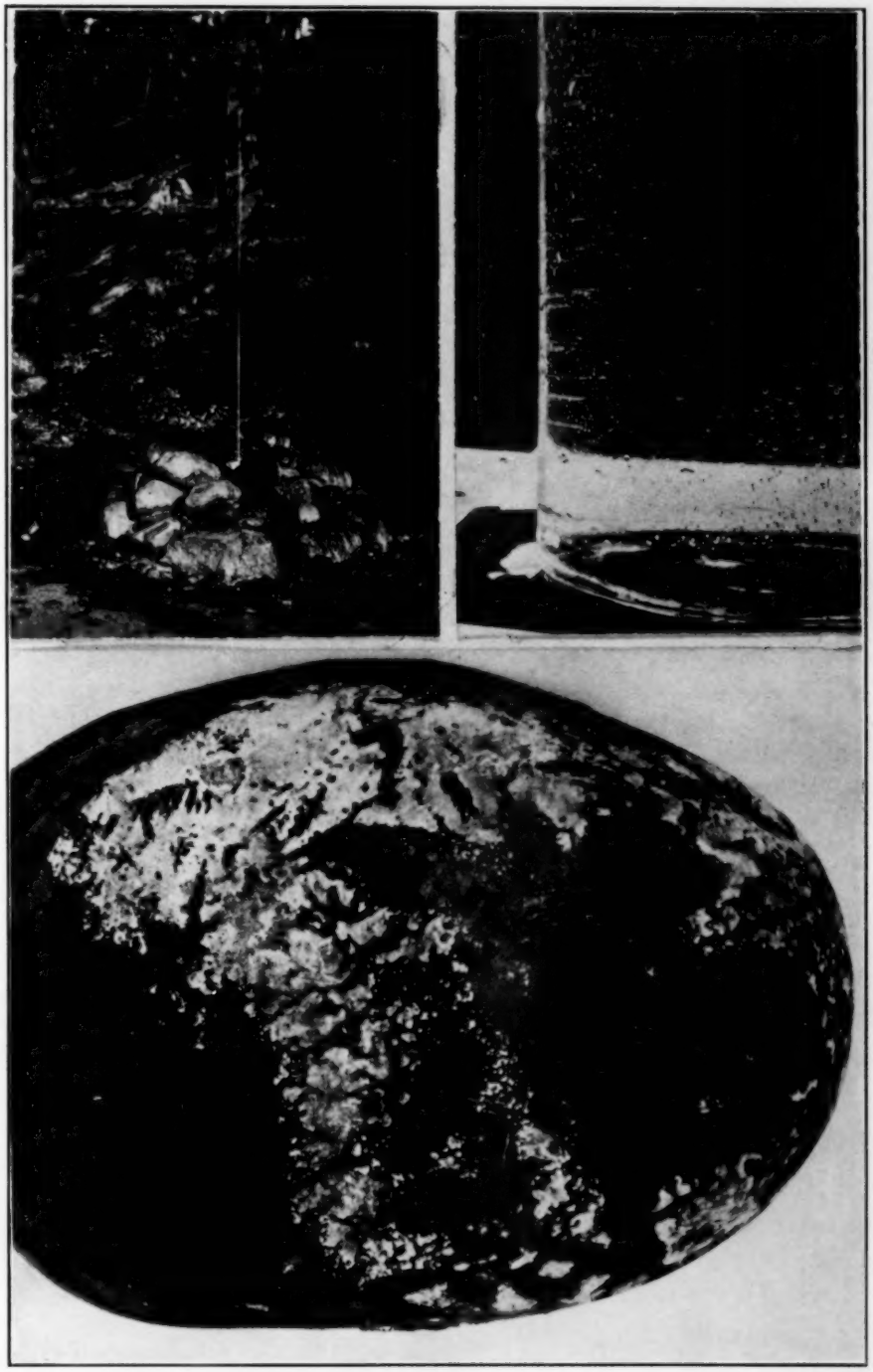
Fig. 3. A stone from the Polaris Spring, showing the calcareous crusts of *Phormidium Demingii*, here appearing white. Natural size.

Plate 25. *Phormidium Demingii*

Fig. 4. Photomicrograph of vertical microtome section through a crust, ×580.

Fig. 5. A teased-out preparation of decalcified material, ×610.

Fig. 6. A similar preparation, ×690.



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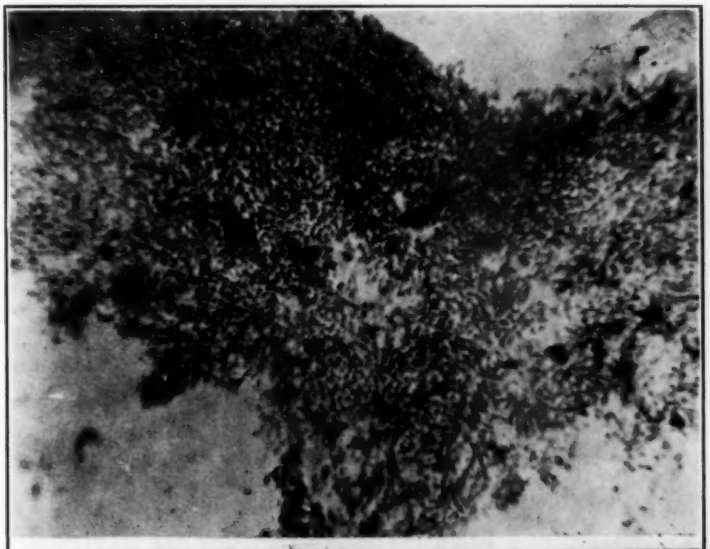

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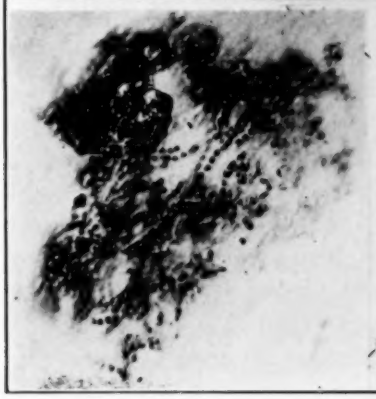

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HOWE: A BLUE-GREEN ALGA

UNIV. OF

On potato catalase

H. H. Bunzell and Marjorie B. Kenyon

(with two figures)

INTRODUCTION

Since the discovery of hydrogen peroxide decomposition by animal and plant tissues (Schönbein, 1863) and the naming of the specific enzyme responsible for this reaction by Loew (1901), much work has been done so that we may learn what rôle catalase plays in the metabolism of plants and animals. The oldest view is that expressed by Loew and later Wieland (1928) that it protects the cells against the hydrogen peroxide formed in the course of photosynthesis and metabolism. For a detailed discussion of the plausibility of this function we refer to the paper of Dakin (1921) and Knott (1927). To date all evidence tending to show the formation of hydrogen peroxide in plant cells is not conclusive and the alleged protective action of catalase is therefore purely speculative.

More suggestive of a definite function of catalase is the work of Appleman (1915) and that of Pope (1932). Appleman studied the catalase activity and oxidase activities of potato juice and simultaneously the intensity of respiration of the tubers from which the juice was obtained. His principal conclusions were firstly, that there is no correlation between oxidase activity and the rate of respiration of the tubers and secondly, that there is a very striking correlation between catalase activity and the rate of respiration of the tubers.

The senior author (1914) studied the oxidases of growing potato plants in Houlton, Maine. The oxidase activities of tubers and foliage toward eighteen different oxidase reagents were determined at different stages of development. In the case of the tubers there appears to be no definite trend of the oxidase activity during growth. The oxidase activity of the foliage of normally developing potato plants is greatest in the early stages of development; it falls off with growth of the plants and rises again when the plants' growth about reaches a standstill. It was also found that the juice of the tubers is in all cases several times as active as the juice of the foliage.

The experiments were carried out by means of the manometric method (1912) for determining oxidases. Quite recently we developed a manometric method for catalase determination (1930a, 1930b, 1932). To learn what relationship, if any, exists between catalase content and oxidase content in growing potatoes, it seemed desirable to carry out experiments similar to those performed in Maine, determining the catalase activity at

different stages of development. The plantings were made by the junior author in Hastings, Michigan.

METHODS

Petoskey Russet potatoes were planted. Great care was taken to have uniform conditions in the soil and in the manner of planting. The plants were pulled at 6:00 A.M., washed with tap water and dried by first gently patting with a linen towel and then hanging in a strong breeze for five minutes. Each plant was then weighed. The leaves were separated from the stems and ground through the "butter knife" of a food grinder. Catalase determinations, Bunzell (1930) method, were run on weighed samples of this pulp so obtained. Catalase determinations were also run on the juice obtained by straining the pulp through fine muslin. The stems and tubers were treated in the same manner as the leaves. Catalase determinations were run on the tubers before planting and also on the pieces of seed tuber adhering to the plant.

RESULTS

Appleman (1910, 1911) found the catalase activity of potato pulp rather unstable. We therefore first performed some experiments showing whether within the duration of the experiment there was marked loss in catalase activity. The results are shown in table 1.

TABLE 1

POTATO PULP			POTATO JUICE		
TIME	MM. OF MERCURY	CATALASE UNITS	TIME	MM. OF MERCURY	CATALASE UNITS
Immediately After Grinding	20.0	1371	Immediately After Grinding	18.0	1234
30 min.	20.0	1371	30 min.	20.0	1371
1 hour	20.0	1371	1 hour	20.0	1371
2 hours	18.0	1234	2 hours	18.0	1234
4 hours	16.0	1097	4 hours	13.0	901

It is evident that in both the potato pulp and the potato juice the catalase activity remains constant, within experimental errors, for at least an hour and soon after that, shows gradual diminution. Inasmuch as our determinations were completed within less than one hour after preparation of sample, no error is introduced through standing.

The catalase content of the various parts of the potato plant at different stages of development is shown in tables 2 and 3 and figures 1 and 2. Table 2 and figure 1 give results obtained on pulp while table 3 and figure 2 on the expressed juice.

TABLE 2

Catalase activities of different parts of potato plant at different stages of development (pulp)

AGE OF PLANT (DAYS)	WEIGHT OF PLANT	NUMBER OF TUBERS	TOTAL WEIGHT OF TUBERS	SEED POTATOES	CATALASE ACTIVITY EXPRESSED IN CATALASE UNITS[a]			
					SHOOTS	LEAVES	STEMS	TUBERS
				14303.7				
15	5.5			14942.5	14563.0			
22	14.4			15211.0		46322.0	17980.0	
29	41.9			13685.0		44615.0	15050.0	
35	66.5					47538.0	14468.0	
43	229.1					60916.0	16613.0	
51	289.6	9	29.7			48230.0	12400.0	19290.0
58	513.9	11	195.6			80986.0	14410.0	22545.0
65	481.0	11	286.2			81300.0	13780.0	20670.0
71	453.6	11	445.8			65468.0	14591.0	19094.0
73	727.9	10	855.4			74680.0	14520.0	23508.0
103								13710.0

[a] Based on oxygen pressure produced by one gram of material in five minutes.

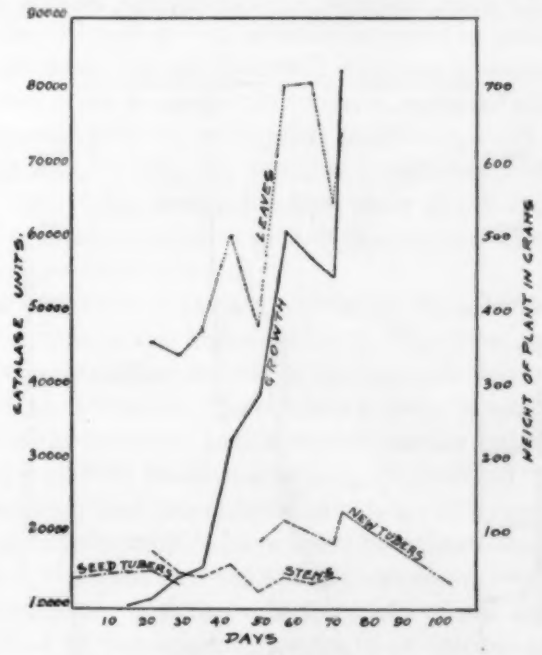

FIGURE 1.
CATALASE ACTIVITIES OF PULP AND JUICE MIXTURE.

DISCUSSION

There appears to be no parallelism between the oxidase activity and the catalase activity when the different parts of the potato plant are sepa-

TABLE 3

Catalase activities of different parts of potato plant at different stages of development (expressed juice)

AGE OF PLANT (DAYS)	WEIGHT OF PLANT	NUMBER OF TUBERS	TOTAL WEIGHT OF TUBERS	SEED POTATOES	CATALASE ACTIVITY EXPRESSED IN CATALASE UNITS [a]			
					SHOOTS	LEAVES	STEMS	TUBERS
				16174.5				
15	5.5			18372.0				
22	14.4			11754.0		41848.4	15190.0	
29	41.9			13685.0		46529.0	13685.0	
35	66.5					45470.0	12400.0	
43	229.1					47071.0	17308.0	
51	289.6	9	29.7			44037.0	13090.0	14465.0
58	513.9	11	195.6			68616.0	13024.0	23338.0
65	481.0	11	286.2			77160.0	12400.0	20670.0
71	453.0	11	445.8			64104.0	12960.0	19094.0
73	727.0	10	855.4			77428.0	13826.0	24988.0
103								13710.0

[a] Based on oxygen pressure produced by one cubic centimeter of juice in five minutes.

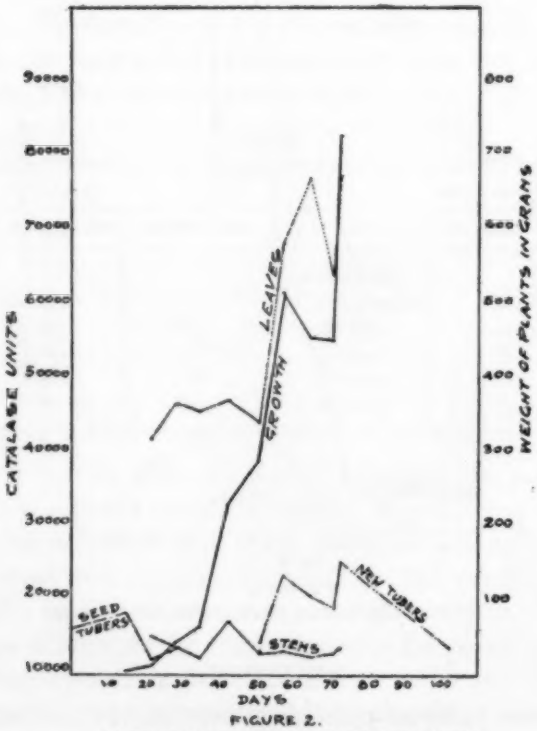

FIGURE 2.
CATALASE ACTIVITIES OF STRAINED JUICE.

rately investigated. The two enzymotic activities certainly do not run parallel, in fact there is some indication that they are in some kind of reciprocal relationship. This latter conclusion is supported by the following evidence.

A. With all oxidase reagents which showed pronounced oxidizability in the presence of potato oxidase, the activity was much greater in the tubers than in the foliage. The catalase activity on the other hand, was constantly two to four times greater in the foliage than in the tubers of the same plants.

B. The oxidase activity of the foliage of healthy potato plants is greatest in the early stages of development; it falls off with the growth of the plants and rises when the plants' growth about reaches a standstill. The catalase activity of the foliage of normally developing potato plants is lowest in the early stages of development, increases with the growth of the plant and diminishes again when the plant reaches full growth.

C. As the average weight of tubers increases from 8.8 grams to 60.0 grams, no constant trend in oxidase activities could be found. The oxidase activity toward some reagents (p-cresol) increases pronouncedly, while it diminishes when other reagents (phloroglucin, resorcin) are used. In case of certain reagents (guaiacol, pyrogallol) there is irregular fluctuation. In the case of catalase activity the situation is different. While very small tubers (3 g.) and fully matured tubers show lower catalase activity, throughout the principal period of growth the catalase activity of the juice of the tubers stays fairly uniform.

This opposite behavior of oxidase activity on the one hand, and catalase activity on the other, is also borne out by the literature. Appleman (1915) finds a slightly lesser oxidase activity in the seed end of potato tubers when compared with the stem end. The catalase activity is much greater in the seed end than in the stem end. In this respect catalase activity runs parallel with respiratory activity which is greater in the seed end than in the stem end. Appleman compared two varieties of potato (McCormick and Carmin no. 1). He found McCormick to have about four times the oxidase activity of Carmin no. 1, while the catalase activity was about twenty-five percent greater in Carmin no. 1 than in McCormick. Ezell and Crist (1927) studied the effect of various plant nutrients on oxidase and catalase activities of lettuce, radish and spinach. In general the oxidase activities fluctuate only within narrow limits, while the catalase activity varies greatly. Reed (1916) in his work on fruit showed that in the process of ripening the catalase activity increased while the oxidase activity stayed constant.

In 1916 the senior author expressed the belief that only a certain por-

tion of a commonly occurring colloidal constituent, such as protein, is responsible for oxidase activity. This active fraction may be in a peculiar colloidal state and the fractional amount of the total may vary from plant to plant and also from one part of a plant to another. It is conceivable that a different degree or type of colloidality would be responsible for the catalase activity. The two types of colloidality would be so interrelated that each operates to the exclusion of the other. In this way a greater catalase activity would be found concurrently with lower oxidase activity and vice versa.

WOMAN'S MEDICAL COLLEGE OF PENNSYLVANIA

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New genera and species of Uredinales[1]

J. C. Arthur

Cumminsiella Arth. nov. gen.

Pycnia subepidermica, paraphysata. Aecia subepidermica, cupulata, peridio instructa; aeciosporae globosae; episporia hyalino, verruculoso. Uredia subepidermica, interdum paraphysata; urediosporae solitarie natae, obovoidae vel subfusiformae; episporio brunneo, verrucoso, poris germinationis equatorialibus vel in series duas dispositis praeditis. Telia subepidermica; teliosporae solitarie natae, 1-septatae; episporio brunneo, verrucoso, quaque cellula poris germinationis 2 lateralibus dispositis praeditis.

This genus is established to segregate from the genus *Uropyxis* those species having subepidermal pycnia and cupulate, aecidioid aecia. So far as known the species of this genus occur only on the genus *Mahonia* of the Berberidaceae and include the three following North American species, the first representing the type: **Cumminsiella sanguinea** (Peck) Arth. nov. comb. (*Uromyces sanguinea* Peck, Bot. Gaz. **4:** 128. 1879, *Puccinia mirabilissima* Peck, Bot. Gaz. **6:** 226. 1881, *Uropyxis mirabilissima* Magn., Ber. Deutsch. Bot. Gessel. **10:** 193. 1892, *Uropyxis sanguinea* Arth., N. Am. Flora **7:** 155. 1907); **Cumminsiella Wootoniana** Arth. nov. comb. (*Uropyxis Wootoniana* Arth., Bull. Torrey Club. **42:** 585. 1915); **Cumminsiella texana** (Holw. & Long) Arth. nov. comb. (*Puccinia texana* Holw. & Long, Bull. Torrey Club **29:** 113. 1902, *Uropyxis texana* Arth., N. Am. Flora **7:** 155. 1907, *Aecidium Butlerianum* Rosen & Arth.; Rosen & Kirby, Phytopath. **9:** 572. 1919.)

Hammarlund, with *C. sanguinea*, now widely distributed in Europe, was the first to establish by cultures the presence of aecidioid aecia in this genus (Bot. Notiser **1930:** 380. 1930; same **1932:** 406. 1932). The assignment of *Aecidium Butlerianum* to *C. texana* is not yet substantiated by cultures. No aecia are known for *C. Wootoniana*.

In general appearance this genus resembles *Puccinia* and produces aecia of the same kind. The shape of the urediospores and the arrangement of the pores as well as the laminate wall of the teliospores with 2 lateral germ pores in each cell seems to indicate relationship with the Uropyxideae-Ravenelieae group of rusts.

The generic name is given in honor of Mr. George B. Cummins who has done commendable work in the taxonomy of the Uredinales.

[1] Contribution from the Botany Department, Purdue University Agricultural Experiment Station, Lafayette, Ind.

Uraecium Arth. nov. form. gen.

Pycnia subcuticularia vel subepidermalia. Aecia sine peridio, interdum paraphysata; aeciosporae pedicellatae.

None of the previously recognized form-genera adequately cares for isolated species having pycnia and uredinoid aecia (so-called primary uredia). The following two species are included in the genus, the first being taken as the type: **Uraecium Holwayi** Arth. nov. comb. (*Uredo Holwayi* Arth., Bull. Torrey Club **33**: 518. 1906; **Uraecium lucumae** (Arth. & Johnston) Arth. nov. comb. (*Uredo lucumae* Arth. & Johnston, Mem. Torrey Club **17**: 169. 1918).

Uredo tacita Arth. nov. spec.

Uredia hypophylla, sparsa, pulverulenta, flavo-brunnea; urediosporae globosae vel ellipsoidae, 19–23×23–28μ, episporio pallide brunneo, 2μ cr., echinulatae, poris germ. 5–8, sparsa.

On *Digitaria Gardesii* (Hack.) Parodi, Mandaque, São Paulo, Brazil, May 25, 1922, E. W. D. & Mary M. Holway *1887*. The host was determined by Dr. A. S. Hitchcock.

Aecidium Hesleri Arth. nov. spec.

Pycnia epiphylla. Aecia hypophylla, maculis orbicularis usque 5 mm. diam. insidentia, gregaria, cupulata; cellulis peridii firme conjunctis, rhomboideis, 15–18×23–30μ; pariete exteriore 4–6μ cr., striato, interiore 3μ cr. verrucoso, aeciosporae globosae, 11–13×13–16μ, episporio 0.5–1μ cr., hyalino, minute verrucoloso.

On *Lithospermum tuberosum* Rugel, near Jasper, Marion Co., along a small stream (Battle Creek), Tenn., May 2, 1931, H. M. Jennison & A. J. Sharp. Communicated by Dr. L. R. Hesler under herbarium no. 350 of the University of Tennessee.

This *Aecidium* differs from the boraginaceous aecia of *Puccinia rubigovera* by its more delicate aecia and especially by the small size of the aeciospores.

PURDUE UNIVERSITY
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A new Piper from British Guiana

WILLIAM TRELEASE

Piper Grahami Trel., sp. nov. Frutex 1.5 m. altus, *P. dilatato* similis; axibus, petiolis, et nervis subtus plus minusve persistenter crispo-pubescentibus; internodiis superioribus gracilibus, satis celeriter elongantibus; foliis subrhombice elliptico-obovatis acuminatis, 7–8 cm. latis, 15–18 cm. longis, in sicco tenues et firmi, basi angustata rotundata in latere uno breviori, nervis pinnatis 5×2, infra medium orientibus, a nervulis transversalibus connexis; petiolis 8–10 mm. longis, 2 mm. crassis, prope basin vaginantibus; spicis obtusis, adhuc 55 mm. longis, 2 mm. crassis, pedunculis vix 5 mm. longis; bracteis rotundato-subpeltatis.

A shrub, 1.5 m. tall, in aspect of foliage resembling *P. dilatatum;* axes petioles and nerves beneath more or less persistently crisp-pubescent; upper internodes slender, rather quickly elongating; leaves subrhombically elliptic-obovate, acuminate, the narrowed base rounded, somewhat shorter on one side, 7–8 cm. broad ×15–18 cm. long, pinnately nerved from the lower half, the nerves 5×2, with connecting cross-veins, drying thin and firm; petiole 2 mm. thick×8–10 mm. long, sheathing near the base; spikes as yet 2 mm. thick×55 mm. long, blunt; peduncle scarcely 5 mm. long; bracts rounded-subpeltate.

Type: Kyk-over-al, junction of the Mazaruni and Cuyuni Rivers, British Guiana, July 9, 1924, *Graham 227*. Graham's field notes give "5 ft. high; aments white when young." Kyk-over-al is a small island in the Mazaruni River where it joins the Cuyuni. The island, which was once cleared by the Dutch who inhabited it and where the ruins of their fortress still stand, was covered with second-growth jungle when the plant was collected.

The species has been named for the collector, Dr. Edward H. Graham, Assistant Curator of Botany at the Carnegie Museum who has in press a local flora of the Kartabo region, British Guiana. The plant is similar to *P. dilatatum* Rich., from which it differs chiefly in the villousness of the nerves beneath and the glabrousness of the leaves above. The type specimen is in the Herbarium of the Carnegie Museum at Pittsburgh, Pennsylvania, with duplicates at the New York Botanical Garden at New York City and at the Herbarium of the University of Illinois, Urbana, Illinois.

Tertiary pollen—II

The oil shales of the Eocene Green River formation

R. P. Wodehouse

(with 56 text figures)

The Green River oil shales of Colorado and Utah are believed to have been deposited in shallow lakes. The conditions under which the deposition took place were such that the pollens which fell upon the surfaces of these waters and sank to the bottom, became permanently imbedded in a translucent gelatinous organic matrix, which later became oil shale, and in which they may be observed today just as they fell, though this took place probably about forty million years ago.

Thus the oil shales hold an ancient pollen record of the same kind as that which forms a part of all pollen surveys today. In pollen surveys microscope slides bearing some transparent adhesive substance, such as glycerine jelly, are exposed out of doors, and every day they are examined and the pollen grains which are caught by the adhesive are identified and counted. In this way the different kinds of pollen floating in the atmosphere of the locality are learned and a record is kept of their abundance from day to day. In the following pages are presented identifications of some of the pollen that floated in the atmosphere and was caught by the Green River lakes in Middle Eocene time.

There are literally thousands of pollen grains in the shales. Frequently they are packed so thickly that they overlap each other making observation difficult. They are far too numerous to permit a complete count of the different species. In the present work only those identifications are recorded which I feel are reasonably certain and close as to the family. These constitute only a relatively small proportion (possibly less than one-third) of the identifiable pollen. The remainder will have to await a considerable extension of our knowledge of pollen morphology. No attempt was made to count the grains of the species which were identified, this is a subject reserved for later study, but in describing each species some note is generally made of my impression of its relative abundance.

In many cases where pollen was identified as belonging to a genus which is already represented in the Green River flora, there is a temptation to refer the pollen to the previously recorded species of that genus. This, of course, cannot be done until the pollen is found in organic connection with the plant to which it belongs. As far as I know this has never been done for pollen from Tertiary deposits, though the reverse is true of much more ancient formations. In fact, most of the known Paleozoic pollen has been

described either from the anthers or pollen chambers of the Pteridosperms and Cordaitales to which they belong. When, therefore, fossil aments or flowers with anthers containing recognizable pollen are found, I would urge that the pollen be examined and carefully recorded, or be submitted to a pollen morphologist to be studied in detail, for only in this way can the pollen species ever be linked with certainty with the fossil plants to which they belong. When this knowledge is gained the value of the fossil record can be enormously extended.

The materials used in these studies consist of nine microscope slides, of which seven are microtome sections of oil shales and two are ground sections of chert concretions from the oil shales. These were very kindly loaned to me for study by Dr. W. H. Bradley of the U. S. Geological Survey. They have already been reported upon by him in his studies of the algae of the Green River formation (15), and more extensively, with a short discussion of their pollen content, in his report on the origin and microfossils of the oil shales (16). In fact, the present paper is an extension of the pollen work initiated there.

The material from which these slides were prepared came from the upper oil shale group of the Parachute Creek member of the Green River formation, most of it from a single group of beds known as "Mahogany Ledge" (see Bradley, 16, pl. 7).

Like all other paleobotanical identifications, those of pollen grains are always made with some uncertainty. The value of all such identifications is exactly proportionate to the degree of probability of their correctness. In the last analysis, the identification of pollen must always be based upon comparisons with living species, or with previously recorded fossil forms, as is the identification of leaves, stems, seeds, and various other parts of plants. The botanist of fossil pollen does not have available reference collections comparable in extent to the large herbaria which are at the disposal of other paleobotanists. Nor has he knowledge of the structures of pollen grains and their phylogenetic significance which is in any way comparable to that which is the common heritage of other paleobotanists with their material. It is to be hoped, therefore, that the value of such pollen-grain identifications as these will be made sufficiently apparent by workers in this field to warrant the building up of collections of permanently mounted pollen slides comparable in extent to the great herbaria of the world, and that capable workers will be attracted to study and to portray the pollen forms, as has been done with other plant structures. Until this gap is filled, the fossil-pollen botanist must build up and interpret his own reference collections to meet his needs as the work of identification pro-

gresses, and the degree of reliability of his identifications will depend largely upon the extent of his collections and his understanding of them.

In the present work I had at my disposal a nucleus collection of two or three thousand slides, prepared and studied by myself, including species of practically all the wind pollinated genera of North America, and many from various other countries. As the work of identification progressed, I added to my collection the pollen of living representatives of the Green River flora (Wodehouse, 46). This was later extended by the addition of pollen of the majority of the living representatives of the entire Eocene flora. My own estimate of the probability of the correctness of the identifications is generally included with the description of each species.

Fossil pollen has been reported from time to time for many years and from most of the geological formations where records of spermatophytes are found. For the most part such reports have been only casual mention of pollen found in connection with other paleobotanical studies. More recently, however, it has become generally known that pollen has been preserved in enormous quantities in post-glacial, and inter-glacial peats, and many such deposits have been intensively studied, particularly in Europe. It is found that the pollen in such peats can be identified with a fair degree of certainty, and from a study of the incidence and distribution of the different kinds in time and space there has been obtained much valuable information regarding the history of the vegetation and climatic conditions in various parts of the world since the Pleistocene glaciation. Though scores of investigators are now working on Recent deposits, only very few have devoted themselves to earlier deposits of similar kind. One of these is Robert Potonié (38, 39, 40, 41). He has described many different kinds of pollen from European Eocene and Miocene brown coals. Some of the pollen species he has found possible to refer to living genera, but the majority are described and illustrated without attempting their identification, for, it is pointed out, even these records, without a knowledge of the identity of the pollen, are valuable in characterizing the brown coals in such a way that they may be recognized by microscopic examination. Potonié says, however, that both wind-borne and insect-carried pollen are found in the coals; though the former might have been blown in from distances, the latter, such as the pollen of the Ericaceae which is found in considerable quantity, must have originated *in situ*. In some of the moors of localities similar to those where the coals were obtained, species of the Ericaceae are growing, and Ericaceous pollen is found in the top layers of the peat. Presumably, therefore, conditions were about the same when the Tertiary brown coals were laid down, as now.

A work similar to that of Potonié is being conducted by Kirchheimer (24, 25). He has described and illustrated many species of pollen from Eocene brown coals and has succeeded in arranging them according to a system modified from the classification of Fischer (23), and some of the fossil pollen he has identified as that of living genera. Apart from these studies I do not know of any other reports on the pollen of Tertiary deposits.

In the work of these and earlier investigators pollen species are always designated as *Pollenites* or *Pollinites* followed by the specific name proposed by the author and preceded by the generic name when this is known or suspected. The use of the world *Pollinites* has the value of pointing out the fact that the object so designated is a fossil pollen grain, but it is without other significance because, designating all pollen, it becomes universal and designates nothing, and its monotonous repetition takes up space to no purpose other than to tell that the fossil, which we already know to be a pollen grain, is a fossil pollen grain. Consequently I propose, and have here adopted, the following system of nomenclature. The word *Pollinites* is retained for its slight value in indicating the general nature of the object under consideration, but it is contracted to '*-pites*' and used as a suffix applied to the specific designation if the genus of the pollen species is known with the normal degree of accuracy, otherwise, to its generic designation. Thus a grain which is certainly that of *Pinus*, and which resembles most closely that of the living *Pinus Strobus*, is called *Pinus strobipites*. And the pollen of *Ephedra*, which is the first record of the genus in the Eocene in America, may be called *Ephedra eocenipites*. But, if the genus is not accurately or certainly known, the termination '*-pites*' is applied to the generic designation of the fossil grain instead of to its specific designation. Thus a grain which is known to belong to the Ericaceae, but the genus of which cannot be determined, is called *Ericipites longisulcatus*, for example, the specific name having reference to the length of its furrows. And a grain that matches the living species of *Smilax* but also matches almost equally well those of some other genera is called *Smilacipites molloides*, for example, its specific designation referring to its further resemblance to the grains of the living *Smilax mollis*. If at some later date any of those genera which bear the termination '*-pites*' should become more closely defined or proved to be accurately determined, the termination may then be transferred to the specific names. The advantages of this system are that complete freedom is allowed in the use of descriptive adjectives as specific names without the introduction of trinomials, some idea is conveyed of the closeness or reliability of the determination, and always is shown the fact that the determination is based on a fossil pollen grain.

Some of the species described here appear to be very similar to some of those described by Potonié and Kirchheimer and indeed may be the same, but for none was I able to prove this entirely to my satisfaction, consequently I have described them all as new. The descriptions are always based upon as many grains as were found suitable for detailed examination, but only a single one is chosen as the type, selected either because I regarded it as most typical or because it seemed to show the characters to the best advantage.

The slides upon which the descriptions are based will be permanently lodged with the U. S. Geological Survey, and in order that other pollen specimens may be compared with those described here, the locations of the holotypes among the slides are indicated after each description by three numbers. The first number designates the slide, the second the ordinate and the third the abscissa reading of the stage micrometer. The stage used was made by Carl Zeiss, known as 'mechanical stage E,' and the divisions of the scale are in millimeters and tenths. If the same type of stage is used and properly centered all of the holotype readings may be readily picked up. In order to facilitate finding the holotypes when other kinds of stages are used, I have supplied a reference point on each of the slides indicated by a conspicuous cross (+). The readings of these are as follows: 3–15.2–54.2; 4–9.7–48.9; 5–20.8–53.9; 6–11.1–48.8; 8–9.5–50.6; 17–13.9–51.0; 36–24.0–73.1; 25/6–14.9–62.7; 25/8–19.5–55.2.

If these readings are compared with the readings for the same points using any other mechanical stage and the numerical differences added to or subtracted from the readings of the holotype, the latter may be found with any microscope which has a mechanical stage providing its micrometer scales are divided into millimeters.

CYCADACEAE

Cycadopites gen. nov.

Essentially as in living species of *Cycas*, but larger. Ellipsoidal, about twice as long as broad, 25–45μ long; provided with a single longitudinal furrow, reaching almost from end to end and always gaping open at its ends, even when tightly closed in the middle. Exine thin but firm, of various texture but generally quite smooth.

In the oil shales are a great many grains of this description. These occur in various conditions of collapse which can be matched among the grains of species of *Cycas* and *Zamia*. That they belong to the Cycadaceae seems tolerably certain, but I have made no attempt to distinguish the different genera and species from each other for this is rarely possible even with living material.

Three grains are figured (figs. 1, 2, 3), but since they possess no differentiating characters, except possibly that of size, they are shown here principally as examples of the various forms of collapse that such grains undergo.

Dioonipites gen. nov.

Spherical or more or less invaginated on one side, 28.5–34.2μ in diameter. Exine rather thick, minutely pitted and of uniform thickness throughout, presenting a radially striate appearance in optical section.

The position of this genus among the Cycadaceae is not certain. Five specimens were found. Three are quite spherical and without any suggestion of a germinal furrow, one has a slight indentation (fig. 4) while the fifth is flattened on one side with a well developed rim which suggests that in life it had a deep furrow (fig. 5). These can be matched in form perfectly with grains of *Dioon spinulosum*, and the latter range in size from 26–29.5μ in diameter. The grains of *Dioon* are exceptional among those of the Cycads in two important respects; their whole surface, including the furrow floor, is finely pitted, and when moistened the evagination of the furrow may be so complete that the grain becomes almost perfectly spherical, showing little or no suggestion of its former furrow. In the pollen of *Dioon spinulosum* which I have examined, grains occur in the three conditions which are represented by the fossil specimens.

The grains of the Araucarineae also bear a marked resemblance to these in form so that there is a possibility that they may belong to that group, but those of the only two species available for comparison, one species of *Araucaria* and one of *Agathis*, are 41–91μ in diameter, much too large to compare with those of the present species.

CONIFERAE

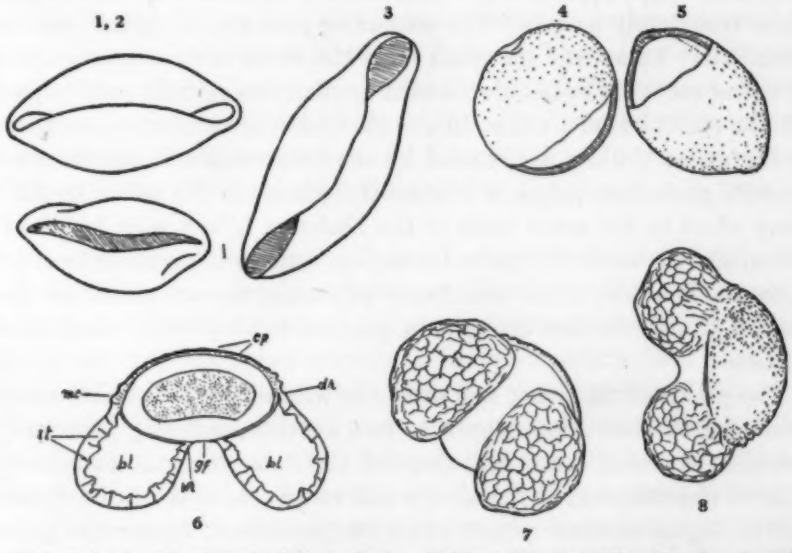
ABIETINEAE

Wherever fossil pollen grains are found those of the Abietineae are generally the most conspicuous and often the most numerous. They have been recorded in the earliest of the Lower Cretaceous floras known from Europe, of the Wealden age, by Graf. Solms-Laubach in his *Pytisporites sp.* from Franz Joseph Land, and by Nathorst in his *Pytisporites sp.* from Scania. And all through the paleobotanical literature of succeeding ages the scattered references to pollen grains that are encountered from time to time generally are concerned with the large and conspicuous winged grains of the Abietineae.

Though it is the winged grains of the Abietineae that have been observed most frequently, not all of the Abietineae have winged grains. As a

matter of fact, on the basis of their pollen morphology the Abietineae may be divided into two groups, the *winged-grained* and the *wingless-grained*. To the former belong *Pinus*, *Picea*, *Abies*, *Cedrus* and *Pseudolarix;* to the latter belong *Tsuga*, *Larix*, and *Pseudotsuga*. The pollen grains of these two classes are remarkably distinct and there are no intermediate forms among living species.

The grains of the winged-grained group are characterized by the possession of two large and conspicuous air-filled bladders (fig. 7), one on



Figs. 1–3, *Cycadopites*. Pollen grains probably of various Cycads, fig. 1, pollen, 45μ long, fig. 2, 26μ long, fig. 3, 37μ long; figs. 4, 5, *Dioonipites*, fig. 4, 30.4, fig. 5, 33μ in diameter, fig. 6, optical section, diagrammatic, of a grain of *Pinus;* fig. 7, *Pinus strobipites* seen from the ventral side; fig. 8, *Pinus scopulipites*, end view.

All figures were drawn from studies made at a magnification of 900, using a Zeiss 3 mm. apochromatic objective, N. A. 1.4, and paired 15× binocular eyepieces. Measurements, excepting those of very large grains, were made at a magnification of 1800, using a 2 mm. apochromatic objective, N. A. 1.3, and a 20× eyepiece. The sizes of the drawings are chosen to best display the characters of the grains and do not bear a constant relation to their dimensions.

each side of the germinal furrow. On this account such a grain possesses bilatical symmetry, and dorsal and ventral sides are differentiated. The ventral (the lower in fig. 6) bears the single germinal furrow (g.f. fig. 6), which extends from end to end of the grain, vertically to the plane of the diagram. It is not sharply defined, consisting merely of a longitudinal strip of thin flexible exine between the two bladders (bl) which flank it on either

side. The bladders are large balloon-like structures which, when the grains are moist and expanded, stand out wing-fashion; hence they are sometimes called wings. They are attached along the margin of the furrow by their ventral roots (vr) and above by their dorsal roots (dr). The dorsal surface of the grain is covered with a layer of very thick and more or less rigid exine, the cap (cp) or disc. The texture of this is peculiar and highly distinctive. It has the appearance of being composed of two or more substances twisted and rolled together, and towards the margin of the cap it is thrown into upstanding convolutions which surround the cap more or less completely as a frill-like projecting rim, the marginal crest (mc). Immediately below the marginal crest the exine of the cap merges into the dorsal roots of the bladders which are morphologically only tangential splits in the thickened exine. In the bladders the curious convolutions of the texture of the cap are carried by the outer wall and are thrown into inwardly projecting ridges, the internal thickenings (it) which lend a stiffening effect to the outer walls of the bladders. When such a grain dries and shrinks the furrow is drawn inwards and upwards, a movement which causes the bladders to become closely appressed to each other forming an effective closure for the furrow, the protection of which is their obvious function.

The grains of the living species of the winged-grained Abietineae bear a remarkably close resemblance to one another, differing principally in their size, the relative size and shape of their bladders, and such less conspicuous characters as the thickness and roughness of the exine of the cap and the degree of development of its marginal crest. In size the grains of the living species which I have observed of *Pinus*, *Pseudolarix* and *Cedrus* range from 48 to 64μ in diameter, exclusive of the bladders, while those of *Picea* range from 68 to 85μ, and those of *Abies* 85–109μ. Measurements of these grains must always be made exclusive of the bladders because the condition of the grain (i.e. the degree of its expansion) at the time of its observation determines the width of separation of its bladders. The grains of *Pinus* and *Pseudolarix* are further characterized by the shape of their bladders which tend to be globular and do not become concaved, or only slightly so, on their proximal surfaces when they are dried and contracted, while the bladders of the grains of *Cedrus*, *Picea* and *Abies* may become decidedly concave as the grains contract.

The grains of the WINGLESS-GRAINED ABIETINEAE cannot be so generally characterized, those of each genus presenting its own peculiar characteristics. Accordingly their further discussion is deferred to the consideration of the various genera.

In the Green River oil shales the grains of the WINGED-GRAINED

ABIETINEAE are the most conspicuous elements, and their preservation is almost perfect. On the basis of their size they fall into three groups, apparently representing the three genera *Pinus*, *Picea* and *Abies*, and a single specimen which conforms more closely to the pollen of *Cedrus*.

Pinus

The numerous grains of the smaller size group (viz. 48–65μ), which are undoubtedly those of *Pinus*, show a rather wide variation in their individual sizes and the degree of development of their marginal crests (figs. 7–9). So much is this so that it is certain that these grains represent more than a single species. On the basis of their size alone they fall into three classes. Accordingly these are provisionally regarded as species. Moreover it is quite possible that each of these provisional species represents more than a single natural species because the grains of different living species of *Pinus* are frequently virtually identical in size as well as in their other characters.

Fossil grains of *Pinus* occur almost wherever fossil pollen is found. They have been recorded from European Eocene and Miocene brown coals (24, 41), and their existence in the Green River shales has already been pointed out (16). Here they occur in enormous numbers; they are the most numerous of all the conifers and among the most numerous pollen grains of any kind. Yet no species of pine is otherwise represented in the Green River flora. Pines are known to have existed since Cretaceous times, and throughout the Tertiary were rather widespread, yet they are not nearly so well represented in the known fossil record as some other conifers such as *Taxodium*, *Tumion* and *Sequoia*. The pollen record of the oil shales suggests that this disparity between the abundance of the fossil pollen and other records of the trees is due to the fact that the pines were upland species not favorably situated for fossilization except through their pollen.

Pinus strobipites sp. nov. (fig. 7). Grains essentially the same as those of the living *Pinus Strobus*, measured across the disc, exclusive of the bladders, 47.9–52μ. Marginal rim marked by a slightly roughened thickening of varying extent. Bladders about 43–46μ in diameter, generally inclined to be globular, but their size, shape, and position, relative to the body of the grain, depending largely upon the degree of its expansion. *Holotype: 36–20.0–61.5.*

These grains are exceedingly abundant in the shales and very uniform, possibly all representing a single species which may have been the same as, or closely related to *Pinus Strobus*, though, as far as the evidence of its grains indicates, it might have been just as closely related to *P. nigra* or *P. attenuata*.

Pinus scopulipites sp. nov. (fig. 8). Grains essentially like those of the living *P. scopulorum*, differing only in the slightly lesser development of the marginal crest, 54–60μ in diameter. *Holotype: 6–11.25–62.5.*

These grains are somewhat less numerous in the shales, than the preceding species. Eight perfectly preserved specimens were examined in detail, and many, less favorably preserved, were observed. One of the outstanding characters, other than that of size, which seems to distinguish this species from the preceding, is the superior development of the marginal crest.

Pinus tuberculipites sp. nov. (fig. 9). Grains essentially like those of *P. tuberculata*, 64–65μ in diameter. Cap approximately circular or squarish in outline, marginal crest well developed, particularly in the regions above the ends of the furrows. *Holotype: 8–13.4–59.2.*

Six well preserved specimens were observed. These are all alike except for the size and shape of their bladders; in one specimen they are relatively large and puffy, while in another they are smaller than is usual with grains of *Pinus*. It is likely, therefore, that the different specimens brought together under the present name represent two or three natural species.

Picea

The grains of the living species of *Picea* are similar to those of *Pinus*, except for their larger size. The three species which I have examined range from 68–86μ in diameter, exclusive of the bladders. The bladders also have a tendency to be flattened dorsiventrally, giving them a pointed appearance when the grain is observed in end view, and as they are pressed together upon drying they may even become concaved over the whole of their proximal surfaces.

Picea grandivescipites sp. nov. As in the generic description (fig. 10).

These are much less numerous than grains of *Pinus*. I was able to find only six specimens that were in a satisfactory state of preservation; they are not all alike and certainly do not all belong to the same natural species, for the smallest measures 70μ in diameter and the largest 85μ. In four of the specimens the bladders are large and puffy, resembling those of the grains of *Pinus*, while in the other two they are smaller and greatly compressed dorsiventrally. These differences in the forms of the bladders, however, are not reliable criteria, and without a larger number of specimens, can have little diagnostic value. They are less significant than the variation in size which alone suggests that the six specimens represent two or three natural species. *Holotype: 4–6.4–70.4.*

Picea is represented in the Green River formation by the single species *Picea pinifructus* R. W. Brn. based on a winged seed. Recognizable fossils of *Picea* are extremely rare throughout the Tertiary formations, but this is probably due to the fact that the trees grew in environments mostly unfavorable to fossilization. Their pollen in the oil shales suggests that they were rather abundant. *Picea-pollenites alatus* Pot. is described from Miocene brown coals of Europe.

Abies

The pollen grains of the living species of *Abies* differ from those of the other winged-grained Abietineae in their larger size. The two living species which I have examined measure about 95 and 107μ in diameter respectively, exclusive of the bladders, and both are characterized by the proportionately much smaller size and more globular shape of their bladders than the grains of either *Pinus* or *Picea*.

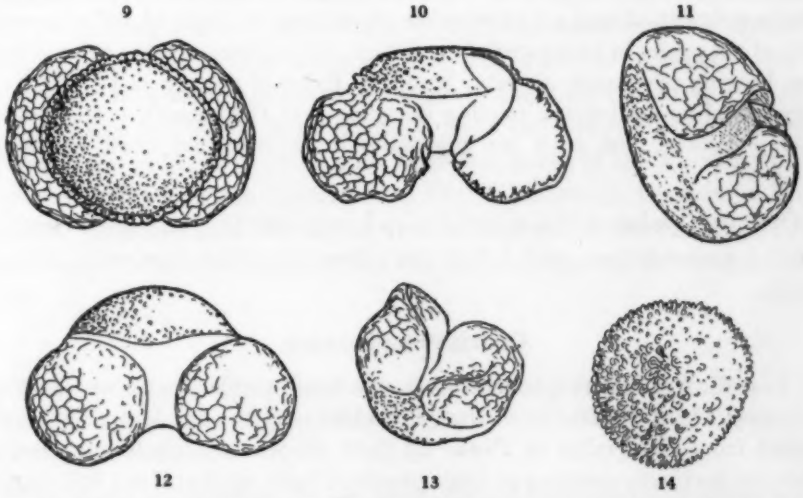


Fig. 9, *Pinus tuberculipites*, dorsal view; fig. 10, *Picea grandivescipites*, end view; fig. 11, *Abies sp.*; fig. 12, *Abies concoloripites*, seen ventrally and from one end; fig. 13, *Cedripites eocenicus*, seen ventrally and from one end; fig. 14, *Tsuga viridi-fluminipites*.

Six specimens which appear to belong to this genus were found in the oil shales. Only the two described below and which are apparently both of the same species, however, could be closely matched with any living species. Of the other four specimens two measure 104μ in diameter; in one of these the bladders are expanded, in the other they are closely appressed against the ventral face of the grain (fig. 11). Another grain measures 143μ in diameter and has bladders large and puffy similar to those of

the grains of *Pinus*. Another measures 140μ in diameter and has only rudimentary bladders. This latter specimen is too poorly preserved to warrant describing it in detail, but its large size, in association with exceedingly weakly developed bladders, suggests that it may represent a primitive member of the Abietineae of a type that is now extinct. These four specimens probably represent four natural species, which either belong to the genus *Abies* or to a closely related genus which no longer exists.

Fossil firs have not heretofore been recorded from the Green River formation and are of extremely rare occurrence in the Tertiary. The presence of these grains, though relatively few, indicates that firs must have been fairly abundant during the Green River epoch for the size of their grains is certainly large enough to seriously impede their dispersal by wind, and would therefore, be expected to greatly reduce their representation in the shales.

Abies concolipites sp. nov. (fig. 12). Grains about 90–110μ in diameter, corresponding in almost all observable characters to those of *Abies concolor*. Body of the grain, in its expanded condition, ellipsoidal or nearly spheroidal in form, bearing two nearly globular bladders. Exine of the cap rather thick and finely granular, its texture passing abruptly into the smooth texture of the ventral surface, but with no suggestion of a marginal crest. *Holotype: 8–13.6–59.5.*

Only two grains of this species were found, but they are in an excellent state of preservation, and I feel that their identification with *Abies* is certain.

Cedripites gen. nov.

Essentially like the grains of *Cedrus Libani*, similar to those of *Pinus*, measuring about 51–56μ in diameter, exclusive of the bladders, but distinguished from the grains of *Pinus* by their proportionately larger bladders which are decidedly concave on their proximal faces, so that if not fully turgid, they have the appearance of closing about the grain somewhat like the two sides of an overcoat, that is too large for the wearer, drawn loosely about the body.

Among the Green River shales was found a single specimen answering this description. The identification of this with the genus *Cedrus*, is of course only problematical, though its peculiar form is not shared with the grain of any other member of the winged-grained Abietineae.

Cedripites eocenicus sp. nov. (fig. 13). Cap 46μ in diameter. Exine rather thick, finely reticulate-granular. Bladders large and flaccid, loosely enveloping the ventral surface of the grain. *Holotype: 8–7.1–65.6.*

Cedrus has not been previously recorded from the Green River formation, nor, as far as I am aware, anywhere in Tertiary deposits. It is, however, known to occur in the Lower Cretaceous of Maryland and its present distribution in Central Asia and North Africa suggests that, like many other Asiatic trees, it may have been one of the American groups that were driven out by the Pleistocene glaciation but was never able to return.

Tsuga viridi-fluminipites sp. nov. (fig. 14). Apparently nearly spherical in life, 78μ in diameter, though in the single specimen found it is flattened in the plane of the section. The entire visible surface of the exine is thick and rather uniformly deeply convolute, giving it a coarsely pebbled appearance. Furrow and bladders entirely lacking. *Holotype: 6-17.7-64.0.*

The size of the grain and the character of its convolutions correspond exactly with the grains of *Tsuga canadensis*. If it could be proved that the lower surface of this grain is similar to the upper—and there is no reason to suppose that it is not—its identification with *Tsuga* would be practically certain. Lacking a knowledge of the under side, however, this specimen might be confused with some fern spore which has a triradiate crest on one side, or with some one-furrowed grain of the Abietineae.

Tsuga has not before been recorded from the Green River formation, nor elsewhere in the Eocene. It does, however, occur in the Miocene Latah formation (9). And its present distribution through temperate North America, Japan, central and southwestern China and the Himalayas suggests that it was probably present in America during the Green River epoch.

Abietipites gen. nov.

Intermediate in form between the grains of *Pinus* and *Tsuga*, provided with a single clearly defined furrow, and a single weakly developed bladder encircling the grain.

This genus is provisionally established to receive species of pollen which appear to belong to the winged-grained Abietineae but do not correspond to any living genus.

Abietipites antiquus sp. nov. (figs. 15, 16). Grains in life apparently lens-shaped or spheroidal, though such is a deduction rather than a statement of fact for the two specimens upon which this description is based are greatly flattened dorsiventrally. Exine of the dorsal surface crinkly granular, exactly like that of *Pinus*, towards the margin of the cap becoming loose in structure and somewhat puffy, and extending beyond the body of the grain as a frill which completely encircles its perimeter. This marginal frill merges with the exine of the ventral surface which is of a loose structure like that of *Tsuga*;

grain provided with a single clearly marked long ventral furrow, more or less tapering, reaching almost or completely across it. *Holotype: 8–6.4–63.7.*

One of the specimens is seen in ventral view (fig. 15) and the other in dorsal view (fig. 16), and both are transparent so that their lower as well as the upper surfaces can be seen. There is considerable difference between the two specimens. The former measures 50.2μ over all and 36.5μ inside the marginal frill (fig. 15), while the latter measures 70μ over all and 45.6μ inside the marginal frill (fig. 16). In the former the furrow tapers at both ends and is not quite as long as the grain, while in the latter it is fully as long as the grain with both ends broad. In the former the encircling frill is of uniform width around the grain while in the latter it is deeply notched in the regions of the ends of the furrows. Though these differences are great enough to make it appear that these two specimens may represent two natural species, the two grains are certainly closely related.

The frill of puffy exine can only be interpreted as a rudimentary bladder. Such structures are common among the spores of various groups as the Pteridosperms, Caytoniales (43) and Pteridophytes, but as far as I am aware, are never found in these groups in association with such a well developed furrow. These specimens appear, therefore, to represent a primitive form of the winged-grained Abietineae. The remarkable resemblance of the texture of its ventral surface to that of the pollen grain of *Tsuga*, among the wingless-grained Abietineae, and of its dorsal surface to that of the grains of the winged-grained Abietineae give it an intermediate position between the winged and wingless-grained groups, and is strongly suggestive of the way in which one of the forms might have been derived from the other.

CUPRESSINEAE, TAXODINEAE AND TAXINEAE

The grains of the living representatives of these three coniferous tribes are alike in many respects, and are at once distinguished from those of the other tribes of the Coniferae by their thin and flexible exine and extremely thick intine. The exine, though always thin, is somewhat various in this respect in the different species. It is always flecked with fine granules; in some the granules are numerous and closely packed; in others they are few, generally irregularly grouped, leaving rather large patches of the exine bare, and often they are easily detachable. The intine which is always of remarkable thickness, is of a hyaline material with a large capacity for absorbing water which causes it to swell enormously, generally with the rupture of the exine, excepting in those grains of which the latter is too thick. The way in which the exine ruptures is a diagnostic character of value, particularly in fossil material where only cast exines are found.

The grains of this plexus of tribes also possess certain characters which serve in living material to distinguish the tribes from each other. In those of the Cupressineae there is never a germ pore or furrow, only occasionally may a vestige of this organ be found. On the other hand among the Taxodineae and Taxineae the germinal furrow is always represented by at least a vestige which, though small, is generally quite conspicuous. In the grains of the Taxodineae it takes the form of a vertically elongate straight or bent papilla, while among the Taxineae it is a broad and meridionally elongate protuberance. Unfortunately, however, in fossil material, the presence or absence of the pore, or furrow vestige, is seldom visible in those grains which rupture easily, for the break generally takes place through the pore. One must, therefore, generally rely for the identification of these upon such characters as the dimensions, the mode of rupture of the exine and the number and distribution of the granular flecks over its surface, characters which make identification, closer to one than another of the three tribes, somewhat uncertain.

In the oil shales are many grains answering the above description making it quite certain that members of one or the other, or possibly all three tribes of this plexus were exceedingly abundant in Green River time. Relatively few of the grains, however, are sufficiently well preserved to reveal the minute and intangible differences existing between those of the different genera. But among them the following can be distinguished with a fair degree of certainty.

Taxodium hiatipites sp. nov. (fig. 17). The split and empty exines of grains which seem in all probability to be those of a species of *Taxodium*. The cleft generally bisects the grain almost completely, but the two halves remain joined at their bases, and opening generally without much buckling though sometimes one of the halves may be crumpled. In size, measured from the tip to the base of one of the halves where it remains joined to its neighboring half, 29.6–37.6μ. *Holotype: 5–12.6–51.6.*

All of the various conditions in which I have found these skins could be exactly matched with the pollen of the living *Taxodium distichum*. The number and arrangement of the surface flecks also match perfectly. There is nevertheless a possibility that these grains might be those of *Juniperus communis* (they are too large for any other species of *Juniperus*) or of *Libocedrus*, though they do not match either quite so well as they do those of *Taxodium*. They are among the most conspicuous pollen elements of the shales; scores of them occur in the sections which I have examined.

Besides the flecked grains there are a few which are quite smooth but otherwise answer the above description. Since it is easily demonstrable

that the flecks of the exine surface are detachable, I am including these grains with the present species on the assumption that they are *Taxodium* grains that have lost their flecks. On the other hand if these grains never had flecks they cannot belong to *Taxodium*. Instead they would match rather well with those of *Thuja* which are only sparsely flecked, or with the grains of some species of *Zamia*, which rupture in this fashion, and are quite smooth. However, bereft of their flecks, grains of this type are reduced to such simplicity that it is without profit to attempt their identification.

A similar grain which I suspect is of the same, or a closely related, species is described as *Pollenites hiatus* Pot. from European Miocene brown coal (41). The name of the present species has reference to the gaping appearance of these empty exines, as suggested by Potonié's name for a similar, if not the same, species.

Taxodium has not been recorded in the Green River flora, unless, perchance the leaves of *Taxites eocenica* R. W. Brn., which Brown (17) states "are suggestive of such coniferous genera as *Taxus*, *Taxodium*, *Tumion*, *Abies*, and *Pseudotsuga*," are to be regarded as such. *Taxodium* belongs, however, to an immensely ancient group whose record dates back to the Cretaceous period. "There are no certainly identified records of ancestral bald cypress in the Cretaceous period, although it is quite possible that some of the similar appearing twigs of fossil conifers that have been referred to *Sequoia* may really be those of an early Cypress." (5). *Taxodium* was of wide distribution in Tertiary times, and is recorded from the Greenland, Wilcox, Fort Union, Jackson and other floras of that period, and in Asia from the Sarmatian flora of Krynka River (35). It is represented in the southern part of North America at the present time by two species, one of which reaches as far north as Maryland. Consequently its presence in the Green River epoch is to be expected.

Glyptostrobus vacuipites sp. nov. (fig. 18). The cast skins of pollen grains, split into two approximately equal halves. Exine in life apparently stiff and under mechanical strain so that, in separating, the two halves buckle with the formation of longitudinal folds. Outer surface dotted with small flecks openly and irregularly spaced. Length of halves 37.6μ. *Holotype: 5–12.6–50.5.*

This grain matches the pollen grains of the living *Glyptostrobus*, which upon rupturing frequently assume this form; they are of almost exactly the same size, and the distribution of the flecks on their surface is likewise the same. It must be admitted, however, that the fossil shows no characters which entirely exclude the possibility of its belonging to some of the other members of this plexus of tribes.

Glyptostrobus, now confined to a small region in central China, belongs to the same ancient group as *Taxodium*. It was wide spread throughout the Tertiary period, and is recorded in the Tertiary Claiborne, Jackson, Wilcox and British Columbia floras, consequently it may be expected in the Green River epoch, though it has not been previously recorded. What has been said regarding the past distribution of *Taxodium* applies equally here, for much of what has been called *Sequoia* appears to be *Glyptostrobus*.

Cunninghamia concedipites sp. nov. (fig. 19). Empty but unruptured exines of pollen grains, 32–37μ in diameter, thin and collapsing irregularly without predetermined folds. Outer surface covered with minute flecks closely but irregularly packed, or smooth. With or without a small rounded papilla. *Holotype: 5–11.1–52.8.*

Six grains were found answering this description, and they match very well with those of the living *Cunninghamia sinensis*. Four of them possess the flecked character of the group and two are quite smooth, but surrounding one of the latter is seen a halo of small granules which had apparently been stripped from the exine. In both of the smooth grains could be seen a minute papilla corresponding to that of the grains of *Cunninghamia*, but in the others no papilla was apparent. But its absence cannot be inferred, for in the collapsed grains of living species of *Cunninghamia* the pore is generally not visible.

The large size of these grains (all except one are over 34μ in diameter) is a character of the *Taxodineae* and precludes the likelihood of these specimens belonging to any of the Cupressineae, for those which I have examined are all under that size. The rather coarse nature of the exine and its mode of collapsing without rupture is quite characteristic of the grains of *Cunninghamia*, so that it is with a high degree of confidence that these grains are assigned to that genus. The specific name of these grains has reference to their customarily collapsed form.

Cunninghamia has not been recorded from the Green River formation, nor elsewhere in the Tertiary, so far as I am aware, but one species, *C. elegans* Corda is recorded from the Upper Cretaceous (3).

GNETACEAE

Ephedra eocenipites sp. nov. (fig. 20). Ellipsoidal, 57–74μ long and about one-half as broad, bearing 5–7 high vertical ridges extending almost from end to end. The grooves between the ridges are each traversed throughout their length by a zigzag hyaline line giving off from its angles short branches which pass outwards into the ridges. Exine thick, smooth and of a horny appearance. *Holotype: 5–14.65–49.8.*

These grains are rather numerous in the oil shales. Six were encountered in an excellent state of preservation and about as many more in a less favorable condition. They correspond in every detail, except their somewhat larger size, with the grains of such living species as *Ephedra glauca* which is about 47μ long, *E. equisetina* Bunge, 53μ, and *E. viridis* Coville, 53μ. In size the six fossil species which were measured are 57, 60, 64.5, 65.6, 68.4 and 74μ long.

The grains of the living species of *Ephedra* are of two types, those with about fifteen low ridges and no hyaline lines in the grooves between them, and those with about five to seven high ridges with distinct hyaline lines in the grooves. It is to this latter type that the fossils all correspond. The size of the grains of any one of the living species is almost constant. The rather great range in size of the fossil specimens, therefore, makes it certain that two or three natural species are involved, and probably none of them is exactly the same as any of the living species. Nevertheless the identity of these with the genus *Ephedra* is rendered certain by their odd and extremely characteristic shape which is not found elsewhere among pollen grains or spores.

Ephedra has not been previously recorded from the Green River formation, nor from the Eocene of America, though it has undoubtedly long been an inhabitant of this continent. But the late Dr. A. H. Hollick had in his possession, shortly before his death, a specimen from the Miocene Florissant which appears to be a fragment of a plant of *Ephedra*, though he had not positively identified it as such. At present the genus is represented in America by six species of low desert shrubs, and at least four of these are found growing in the immediate vicinity of the Green River formation. The majority of the species are now Asiatic, a fact which is strongly suggestive of their American existence during Tertiary time.

NAJADACEAE

Potamogeton Hollickipites sp. nov. (fig. 21). Spheroidal, somewhat ellipsoidal, ovoidal or variously irregular, 16–27.4μ in diameter. Exine rather thin and conspicuously reticulate with a coarse network of beaded ridges. Without pores or furrows, or vestiges of them. *Holotype: 3–7.9–43.7.*

These grains are fairly common in the oil shales; ten perfectly preserved specimens were found and examined in detail. Besides these ten grains there are a number of others of which less than the whole surface can be seen; therefore, it is not known for certain whether they have a germ pore or not, the absence of which is the only character which distinguishes these grains from those of *Sparganium* and some species of *Typha;* but I do not feel that any of these belong to the *Typhaceae*, for

the latter produce pollen in enormously larger quantities than the *Najadaceae* and would therefore be expected to greatly outnumber them in the shales, if the plants had been present.

Potamogeton has not been previously recorded from the Green River formation, but it is represented in the Eocene Wilcox (10), Jackson (6), Miocene Latah (29) and Florissant (26, 18) floras, and, since the latter is regarded as a derivative of the Green River flora, it is to be expected that *Potamogeton* lived during the Green River epoch. It is known to have occurred in the Tertiary Siberian flora (32), and in the Tertiary Samartan flora of Krynka River (35), so its presence in the oil shales points to the northern connections of the Green River flora.

The habits of *Potamogeton* are similar to those of *Myriophyllum* (q.v.), and the presence in the oil shale of its pollen which appears to be mainly insect borne and not likely to be carried far from its point of origin, is interesting in suggesting the nature of the conditions under which the shales were deposited.

The specific name of the present species is in honor of the late Arthur Hollick, Paleobotanist.

ARECACEAE

Arecipites gen. nov.

Ellipsoidal, 23–25μ long, with a single longitudinal furrow which may close tightly throughout its entire length, not gaping at its ends. In form and structure resembling the grains of *Phoenix dactylifera* (44).

It is with some hesitation that these grains are referred to the Palm family on account of the widespread distribution among primitive floras of species with one-furrowed grains of this general character, with which they might be confused. Of such a character are the grains of the Magnoliaceae, Cycads, *Ginkgo* and Bennettitales, but, as far as my experience goes with such forms, the small size of these fossil grains precludes the possibility of their belonging to the Magnoliaceae, and the pointed ends of their furrows do not match the broad rounded ends of those of the Cycads, *Ginkgo* or the Bennettitales.

Four species or Arecaceae have been recorded from the Green River formation (11, 27), and they are known to have grown in great profusion in many regions throughout the Tertiary period.

Arecipites punctatus sp. nov. (fig. 22). Exine minutely pitted but appearing, except under the most favorable conditions, to be quite smooth.

The single specimen which was found matches the grains of *Phoenix dactylifera* in every respect except its somewhat larger size,—the latter range from 19.4–23.9μ in length. *Holotype: 8–11.0–61.4.*

Arecipites rugosus sp. nov. (fig. 23). As in the generic description, except that the exine is decidedly roughened and appears to have transverse striae. *Holotype: 36–8.0–58.6.*

A single specimen of this species was observed. The furrow is deeply invaginated, and its floor may be seen through the transparent exine, though its margins are pressed tightly together. This grain, in size and structure, corresponds with those of the Arecaceae, but in texture does not correspond with any species with which I am familiar. It is therefore somewhat doubtful if it is correctly assigned to the family.

ARACEAE

Peltandripites gen. nov.

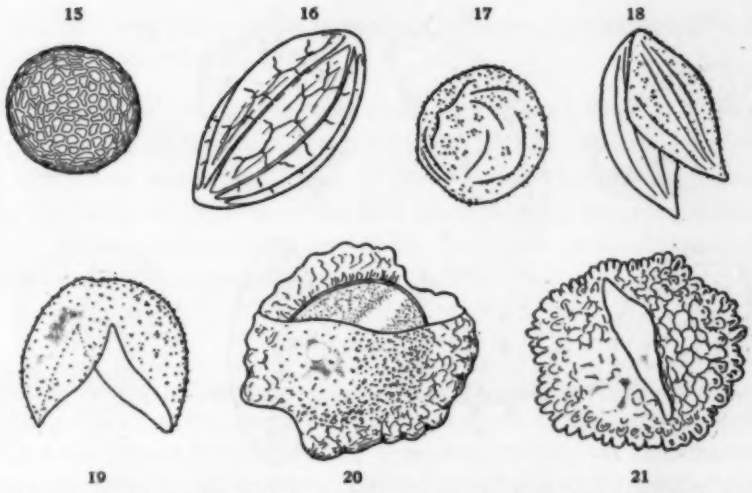
Ellipsoidal, without germinal furrows or pores. Exine rather thin and of smooth texture, but provided with numerous sharp conical spines somewhat irregularly arranged, often obliquely attached and of varying length. As seen in optical section the exine appears to be slightly roughened on its inner surface.

Peltandripites Davisii sp. nov. (fig. 24). 40×35.3μ. Spines averaging about 2.3μ long. *Holotype: 4–10.0–61.6.*

A single specimen of this species was found. It matches with the grains of *Peltandra virginica* Kunth, except for its slightly larger size and slightly more numerous spines. The grains of the latter species are 30–35.3μ in diameter; their spines are of the same size and general appearance as those of the fossil species, though less numerous and more regularly arranged. In these two latter characters the fossil species is intermediate between the grains of *Peltandra* and *Smilax herbacea*, the only other species with which it compares at all closely. The fossil species, however, is much larger than the grains of *S. herbacea* and its spines longer.

Peltandra has not been previously recorded from the Green River formation nor elsewhere in fossil form as far as I am aware, but the Araceae are represented in the Tertiary by *Acoris* in the Florissant and Wilcox floras, by *Pistia* in the Wilcox and Jackson, and by *Arisaema* in the Latah. I feel that the assignment of this grain to the Araceae is certainly correct, but its identification with *Peltandra* is not entirely certain for I have not had opportunity to compare it with many other members of the family. It does not, however, match with the pollen of *Symplocarpus*, *Anthurium*, *Calla* or *Arisaema*.

The specific name of the present fossil species is in honor of Charles A. Davis who prepared most of the slides upon which this work was done, but whose untimely death in 1916 prevented him from studying them.



Figs. 15, 16, *Abietipites antiquus*, fig. 15, ventral view of a grain 50.2μ over all, fig. 16, dorsal view of a grain drawn as if part of the surface were removed to show its appearance in optical section, 70μ over all; fig. 17, *Taxodium hiatipites;* fig. 18, *Glyptostrobus vacuipites;* fig. 19, *Cunninghamia concedipites;* fig. 20, *Ephedra eocenipites;* fig. 21, *Potamogeton Hollickipites.*

LILIACEAE

Smilacipites gen. nov.

Spherical or ellipsoidal, 19–25.8μ in diameter, without a germ pore or furrow. Exine rather thin and, in life, apparently readily deformed by pressure; variously adorned, provided with large or small spines or wart-like granules, texture smooth or only faintly granular.

I have compared these fossils with the pollen of three living species of *Smilax*. The grains of the latter are all spherical, thin walled and variously adorned. That of *S. herbacea* L. is 25–27μ in diameter and provided with sharp conical spines, that of *S. populnea* Kunth, is about 19–20μ in diameter, provided with large wart-like protuberances, and that of *S. mollis* Willd. is about 17μ in diameter, and provided with small papillae. There is much variation in the size and development of the surface adornments even among the grains of the same species and they are always irregular in arrangement. The texture of the exine is otherwise quite smooth.

Though at least one of the fossil species matches perfectly with one of the present day species of *Smilax*, it is not entirely safe to assign any of these fossils unreservedly to the genus *Smilax*, for the same form of grain is known to occur in a number of other groups. For example it is almost exactly duplicated in the Araceae, and, except for size, in *Gnetum*, and is rather closely approached in the Lauraceae and Musaceae.

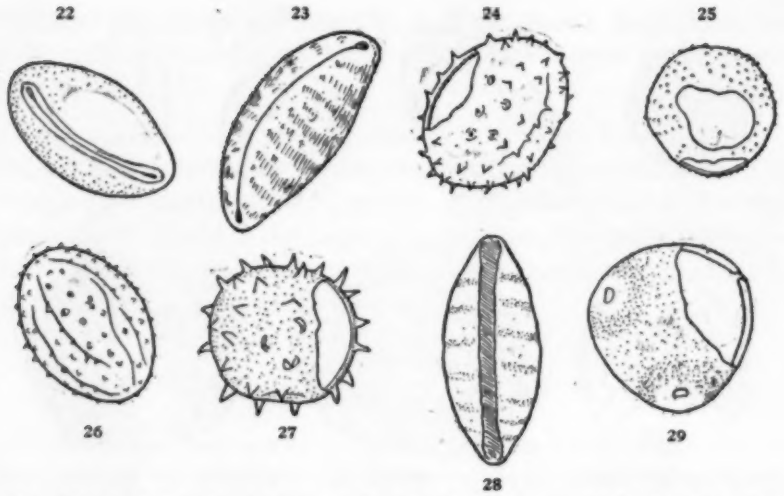


Fig. 22, *Arecipites punctatus;* fig. 23, *Arecipites rugosus;* fig. 24, *Peltandripites Davisii*, drawn as if part were removed to show its appearance in optical section; fig. 25, *Smilacipites molloides*, the upper part of the grain has been sliced off by the microtome, and the remainder is drawn as if a piece were removed from one side to show its appearance in optical section; fig. 26, *Smilacipites herbaceoides;* fig. 27, *Smilacipites echinatus*, drawn as if a part were removed from one side to show its appearance in optical section; fig. 28, *Liriodendron psilopites*, ventral view; fig. 29, *Hicoria viridi-fluminipites*, ventral view, drawn as if a part were removed, to show its appearance in optical section.

Smilax has not previously been recorded from the Green River formation, but one species is found in the Eocene of the Atlantic Coastal Plain, and another from the Tertiary Samartan flora of Krynka River (35), and many are recorded from the Cretaceous to Pliocene of other regions. (6, 9, 10).

Smilacipites molloides sp. nov. (fig. 25). As in the generic description, 19.4μ in diameter. Exine papillate, but texture otherwise smooth. Single specimen found matches exactly with *Smilax mollis* from which its specific name is derived. *Holotype: 3–8.7–41.6.*

Smilacipites herbaceoides sp. nov. (fig. 26). Ellipsoidal, 27.4μ long, but the exine is wrinkled so that the grain was probably less ellipsoidal in life. Provided with small irregularly arranged sharp spines. *Holotype: 8–11.9–63.6.*

This specimen differs from the grains of *S. herbacea* only in its elongate form and smaller spines. The only other genus that this might belong to is *Peltandra*. In the latter, however, the spines are more regularly arranged and the exine is a little thicker.

Smilacipites echinatus sp. nov. (fig. 27). Spheroidal or approximately so, 28.5μ in diameter. Exine rather heavy, finely and vaguely granular, or smooth,

provided with long sharp spines irregularly arranged, averaging about 3.4μ in length. *Holotype: 3–7.8–42.8.*

The spines of this species are more pronounced than is usually the case with grains of *Smilax*. It is to this fact that the specific name refers. Two specimens were found. One of these shows the granular character rather distinctly while in the other it is absent. If the granular character is natural, as it appears to be in one of the specimens, it would preclude the possibility of its belonging to the genus *Smilax*.

MAGNOLIACEAE

Liriodendron psilopites sp. nov. (fig. 28). Ellipsoidal, 62.5×23.5–80 ×38.8μ, provided with a single longitudinal furrow. In the partially expanded condition the furrow is rather broad, of uniform width, not tapering towards its ends, its margins slightly wavy. Exine rather thick and apparently rigid in life, of smooth texture but slightly undulating. It is to the smooth texture of these grains that the specific name refers. *Holotype: 17–11.9–69.5.*

Three specimens of this species were found, and the one that is seen to best advantage (i.e. in ventral view showing the furrow) matches the grain of the living *Liriodendron Tulipifera* in every character except the texture of its exine. In the grains of the living species the exine presents a minutely pitted and somewhat warty appearance. In the grains of other living Magnoliaceae, however, such characters are only of specific value, both smooth and rough grains being found in the same genus. It seems most likely, therefore, that the present fossil is the grain of an extinct species of *Liriodendron*. There is also a possibility, however, that it might belong to some member of the Magnoliaceae that I have not examined, or even to some species entirely unrelated, for one-furrowed grains were much more common among the primitive floras than they are today.

Liriodendron is known to have occurred in the Upper Cretaceous and several species have been recorded from the Eocene (8, 36) and the Miocene (9) formations, consequently it is to be expected in the Green River epoch.

JUGLANDACEAE

Pollen grains of the Juglandaceae are abundant and among the most conspicuous in the oil shales. But owing to the exceptionally wide range of form embraced by the pollen of the various genera of this family, they are not easily identifiable, excepting the conspicuous grains of *Hicoria* and *Juglans*. Consequently, in order that the identifications may be fairly evaluated, I give the following short summary of the pollen characters of

some living Juglandaceae which are likely to be represented in Tertiary formations.

The characters which they share with each other are the smooth or slightly granular character of their exine, their lack of germinal furrows, and their possession of rounded or slightly elongate germinal apertures always surrounded by subexineous thickenings. In the grains of all, except *Hicoria* and *Juglans*, the pores are approximately equally spaced around the equator as in the grains of the Betulaceae, but in the grains of *Hicoria* and *Juglans* the pores are mostly crowded into one hemisphere (the ventral) leaving the greater part of the other (the dorsal) blank. Also in the grains of these two genera the subexineous thickenings of the pores possess but little thickness and do not cause the pores to protrude noticeably above the surface of the grain; instead, they possess greater lateral extension. In the grains of most species of *Juglans* the subexineous thickenings do not quite touch each other, but in those of *Hicoria* they not only touch but are completely fused, forming a continuous sheet underlying the exine of the whole of the ventral hemisphere and all but a small central area of the dorsal hemisphere. On account of these two characters, the one-sided arrangement of their pores and their broad flat subexineous thickenings surrounding them, the grains of *Hicoria* and *Juglans* are easily recognizable. Not so, however, with the grains of such other genera as *Engelhardtia*, *Pterocarya* and *Platycarya;* their pores are arranged around the equator, their subexineous thickenings are abrupt and their pores protrude as in the grains of the Betulaceae which they resemble closely, and, to a lesser extent, some of the Urticaceae, such as *Momisia;* and indeed it is often difficult to distinguish the grains of these families one from the other except through a knowledge of their specific characteristics. The grains of *Pterocarya* range from about 27–36μ in diameter. They are rather distinctive in usually having five or six pores, rarely four, and almost never three. The pores are narrowly elliptical in shape and arranged around the equator with their major axes converging in pairs. They resemble the five-pored grains of *Alnus* in almost all respects except that they lack the connecting bands which characterize the grains of that genus. There is, however, not much likelihood of confusing the grains of the two genera even if the bands do not show, because the majority of *Alnus* grains are four-pored, while the majority of *Pterocarya* are five- or six-pored.

The grains of *Engelhardtia spicata* are almost the same as those of some of the Betulaceae, especially *Corylus*. In fact there is great danger of confusing them. They are, however, about 19–22μ in diameter, which is somewhat smaller than those of *Corylus* or other Betulaceae.

The grains of *Platycarya* are similar in form to those of *Engelhardtia*,

but are smaller, measuring only 14μ in diameter and their apertures are narrow and almost slit-like. A further discussion of the grains of this family in comparison with those of the Betulaceae will be found under that family.

Hicoria

In the oil shales are a large number of pollen grains which are undoubtedly those of *Hicoria;* they differ from living species only in their size. The two fossil species which I have distinguished range from 31.2 to 39μ in diameter, while the grains of the living species which I have examined ranged from 42 to 52μ in diameter. The fossil grains were apparently lens-shaped in life, though the specimens are greatly flattened dorsiventrally. They have three pores confined to the ventral surface, and their exine is smooth or slightly granular particularly around the pores.

The hickories are represented in the Green River flora by a single known species, *H. juglandiformis* (Sternby) Knowlton, a species which also occurs in the Miocene Latah and Florissant formations, and was apparently wide-spread and abundant in Tertiary times. It is therefore quite possible that one or the other of the two following fossil grains belongs to that species, though by no means certain, for in Tertiary times the genus was represented by a number of other species. For example there are recorded two in the Jackson Flora, one in the Claiborne (6), and Wilcox (10) and two in the Tertiary of British Columbia (8). Any or all of these might have been present in the Green River flora, though not yet recorded. Furthermore it is quite possible that the two fossil grains described below represent more than two natural species, for the forms of the various living hickories are not usually distinguishable from each other.

Hicoria viridi-fluminipites sp. nov. (fig. 29). Oblately flattened and rounded triangular in outline, 36–39μ in diameter; pores 3, near the equator of the grain, circular or slightly elliptical with their long axes directed meridionally, 2.3–3.4μ long. *Holotype: 5–17.5–45.0.*

This grain is unquestionably that of a species of *Hicoria.* It matches in all respects, except its smaller size, that of *H. Myristicaeformis.* Therefore it probably represents a species which does not exist at the present time but was related to the *Myristicaeformis* group of hickories. It occurs in the oil shales in great abundance and many of the grains are perfectly preserved. Its specific name refers to the fact that it is a characteristic form of the Green River shales.

From the Miocene brown coals of Europe a similar form of grain is described as *Pollenites globiformis* by Potonié (41), which may be the same species.

Hicoria juxtaporipites sp. nov. (fig. 30). Similar to the preceding, 31.2μ in diameter; pores circular, 2.3μ in diameter, not close to the equator, closer to each other and arranged in a triangle. Exine fine granular. *Holotype: 5–13.1–41.9.*

A single grain of this species was found. It is less like any present day species than is the preceding, but is included here because it undoubtedly belongs to the family and is more like the grains of *Hicoria* than those of any other existing genus.

Juglans nigripites sp. nov. (fig. 31). Grain apparently lens-shaped in life, though the fossil is greatly flattened dorsiventrally in the plane of the section, 40μ in diameter. Visible pores eleven, short elliptical, about 2.2μ long, eight of them are on or nearly on the equator and three on the ventral (lower) surface, but none on the dorsal. Exine rather thick and slightly thicker around the pores, texture finely and faintly granular. *Holotype: 5–17.2–45.4.*

A single specimen of this species was found. It is in a perfect state of preservation and, owing to its transparency both sides are visible. It may, however, have twelve instead of eleven pores. It belongs unquestionably to *Juglans*. It cannot, however, be matched exactly with any living species of which pollen is available. In size it compares favorably with *J. regia* 41.6μ in diameter, but the pores of the latter are circular and larger, 3.3μ in diameter, and fewer in number, 6–11, generally fewer than eleven. On the other hand the pores of the fossil are more numerous than those of *J. cinerea* (5–8). The fossil matches the grains of *J. major*, *J. californica* and *J. nigra* about equally well, though it is too small for any one of these; their sizes are about 34.2, 36.5 and 34μ in diameter, respectively.

Juglans is represented by five known species in the Green River flora, but it is, at present impossible to state to which, if any of these, this fossil grain belongs. *Juglans* is an ancient group, with a history dating back to the Upper Cretaceous (3). In the Tertiary it was represented by many different species and is a conspicuous feature of most of the Tertiary floras, particularly those of the more northerly and colder climates, as for example the Siberian (33), Sakhalin Island (32), and Greenland floras; and in America it occurs in the Denver (31), Wilcox (10) and Raton (36). In the warmer floras it is represented by only a single species in the Claiborne and is absent from the Jackson.

Engelhardtia corylipites sp. nov. (fig. 32). Oblately flattened, triangular in outline, 21.1–23μ in diameter; pores three at the angles, pore diagram as in *Corylus* (fig. 38), with the rim slightly roughened inside. Exine smooth. *Holotype: 3–12.0–44.0.*

Only two specimens of this species were found. They match exactly the grains of *Engelhardtia*, except for a slight difference in size (those of *Engelhardtia spicata* range from 19.4–21.6μ) which is not significant. Nevertheless it is with some hesitation that these fossils are assigned to this genus, because it is only their small size which distinguishes them from the grains of the species of *Momisia* and *Corylus* which I have examined, so they may match as closely some species of these or even other genera that I have not

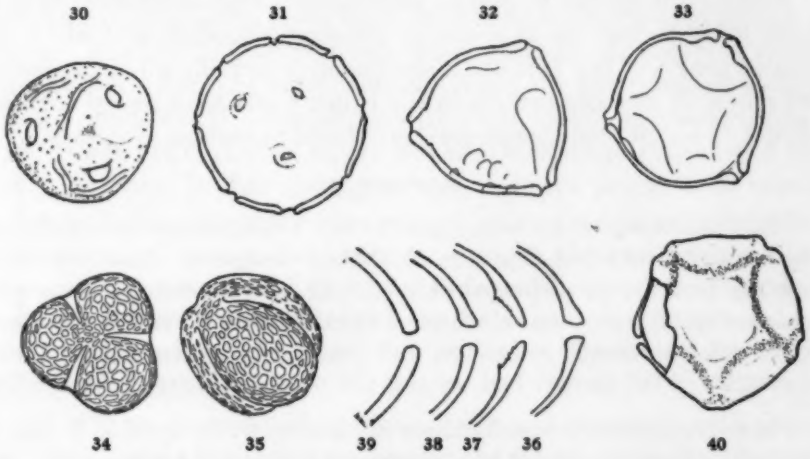


Fig. 30, *Hicoria juxtaporipites*, ventral view; fig. 31, *Juglans nigripites*, optical section. Three pores occurring on the ventral surface, which can be seen through the grain, are dotted; fig. 32, *Engelhardtia corylipites*, optical section; fig. 33, *Myricipites dubius* optical section; figs. 34, 35, *Salix discoloripites*, fig. 34, polar view, fig. 35, side view; figs. 36–39 pore patterns as seen in optical section, of some aspidate grains; fig. 36, "broad-knob" or *Betula* pattern; fig. 37, the *Tarsus* or *Myrica* pattern; fig. 38, the *club-shaped* or *Corylus* pattern; fig. 39, the "unexpanded" or *Carpinus* pattern; fig. 40, *Alnus speciipites*, drawn as if a part were removed, to show its appearance in optical section.

yet seen. Their specific name refers to the resemblance that these grains bear to those of *Corylus*.

Engelhardtia has not previously been recorded from the Green River formation, but it is to be expected there because it is represented in the Florissant of Colorado (18), which is regarded as a Miocene derivative of the Green River flora. It has also been recorded from the Eocene Wilcox (10) and Jackson (6) floras.

MYRICACEAE

Myricipites gen. nov.

Approximately spheroidal. Pores three, greatly protruding, of the tarsus pattern (fig. 37). Texture smooth.

Myricipites dubius sp. nov. (fig. 33). Grains 25.1μ in diameter. Texture of the present specimen wrinkled but probably smooth in life. *Holotype: 25/8–13.2–49.4.*

Only a single specimen of this species was found and it is badly shrunken and wrinkled. My reason for assigning it to *Myrica* is based principally upon the character of the thickenings surrounding the pores. In the present specimen, however, this appearance may be due to its shrunken condition.

About eight species of *Myrica* have already been distinguished in the Green River formation. It is one of the most abundant and widely distributed genera of the Tertiary, occurring in practically all of the floras of that epoch. It was also present in the Upper Cretaceous period (3) and is still widely distributed though greatly reduced in number of species.

SALICACEAE

Salix discoloripites sp. nov. (figs. 34, 35). Tricolpate and generally more or less deeply three lobed, isodiametric, slightly elongate or oblately flattened, according to the degree of expansion; 13.7–23.9μ in diameter. Furrows long and tapering, without internal marginal thickenings and without germ pores. Exine thick and coarsely reticulate, with the network generally finer towards the margins of the furrows and towards the poles. *Holotype: 5–14.25–44.9.*

These grains match exactly those of the two living species, *S. discolor* and *S. fragilis*, with which I have compared them, and I know of no other grains, other than those of willow, with which they could be compared,—their lack of germ pore and furrow thickenings seems to be distinctive. These grains are extremely numerous, possibly the most abundant of any species in the shales. In view of the fact that the willows are primarily insect pollinated and are not profuse pollen shedders, the large numbers of their grains found in the shales attest to the enormous abundance of the willows in the Green River epoch and their proximity to the place of deposition. The suggestion naturally occurs that possibly these grains belong to some species closely related to *Salix* but which is wind pollinated, for example *Populus*. In this connection, therefore it should be pointed out that the pollen grains of *Populus* bear no resemblance to those of *Salix* and could not possibly be confused with them. No grains of *Populus* were found in the oil shales though the trees are enormously productive of pollen and are believed to have flourished abundantly during the Green River epoch. The grains of *Populus* are provided with only a thin, almost fragmentary, exine, and I suspect that their absence from the Green River shales is attributable to their fragile nature.

Four species of *Salix* have been recorded from the Green River formation (17, 27) and one from the Wind River Basin of Wyoming of Green

River age (11); willows are also common in other floras of Tertiary age. What appears to be the pollen of the same species as the present one is described by Potonié (40) as *Pollenites fraudulentus* Pot. from Eocene brown coal of Germany.

BETULACEAE

The grains of the living Betulaceae are smooth or only faintly granular, spheroidal or more or less oblately flattened, 20–35μ in diameter, provided with three to seven germ pores which tend to be equally spaced around the equator. In shape the germinal-apertures differ in the different species, being circular, elliptical or slit shaped. When the apertures are elongate they are meridionally oriented, or with their major axes converging in pairs, if there are more than three. The most distinctive character of these grains, however, is that their germ pores always protrude as rounded domes, and give the grains when seen in polar view an angular outline. This character I have called 'aspidate' owing to the resemblance of such a protruding pore to a small circular shield or *aspis*. The dome-shaped protrusions are due to a thickening of the intine underlying the region immediately surrounding the pore, and frequently also to a lesser annular thickening of the exine.

All of these characters the grains of the Betulaceae share with those of the Myricaceae, *Myriophyllum* among the Haloragidaceae, *Platycaria*, *Engelhardtia* and *Pterocarya* among the Juglandaceae, and *Momisia* among the Ulmaceae; and they closely resemble the grains of *Broussonetia*, *Morus*, *Humulus* and *Cannabis* among the Urticaceae. In fact they represent a form towards which the grains of many wind-pollinated species of diverse origins tend to approach. This, together with a close intrafamily resemblance of the various genera makes the recognition of the pollen grains of the Betulaceae always difficult and occasionally uncertain.

They can generally be distinguished, however, by certain minor characters which they possess individually. One such character is found in the annular thickening of the exine surrounding the pore. When seen in optical section with the pore at the plane of focus, the germinal aperture appears as a gap at which the walls on either side end with knob-like thickenings, which vary in the different species.

Passing in review the grains of the members of the Betulaceae and those of families with which it is possible to confuse them, four fairly well marked types of pore pattern may be distinguished. These are (1) the broad-knob or *Betula* pore pattern (fig. 36) in which the exine appears in optical section to end at the pore in a broad and abrupt expansion, and the pores, as a consequence of the thickening of the exine, are raised sharply above the

surface of the grain. This pore pattern is characteristic of all species of *Betula*, *Myriophyllum* and, with a slight modification towards the next type, of *Alnus*. (2) the tarsus or *Myrica* pore pattern in which the wall thickness suggests in appearance the shape of the terminal joint or tarsus of the hind legs of some insects (fig. 37). This form in its fullest development characterizes the grains of *Myrica* and *Comptonia*, and is somewhat approached in those of *Engelhardtia* and *Alnus* (3), the club-shaped or *Corylus* pore pattern (fig. 38) in which the exine is only slightly and gradually expanded at the pores; consequently in such grains the pores are only slightly raised above the surface. This form characterizes the grains of *Corylus*, *Pterocarya*, *Platycarya* and *Momisia*, and, with a certain tendency towards the tarsus pattern, those of *Ostrya* (4), the unexpanded or *Carpinus* pore pattern (fig. 39). In this the walls of the exine are not at all or only very slightly expanded at the pores. It must be admitted the distinction between this and the previous pore pattern is often vague. This pattern characterizes the grain of *Carpinus* and, with a modification towards the tarsus type, that of *Engelhardtia*. Fortunately we are further aided in the identification of these two grains by the fact that that of *Carpinus* is the largest while that of *Engelhardtia* is the smallest of all of the grains possessing this pore pattern.

Alnus speciipites sp. nov. (fig. 40). Lens-shaped, 20–30.4μ in diameter; pores 4 or 5, occasionally 3 or 6, arranged around the equator with the long axes of their apertures which are elliptical converging in pairs. Exine smooth or slightly roughened, greatly thickened in the region immediately surrounding the pores causing them to protrude markedly (fig. 36) and giving the grain an angular appearance. The exine is also thickened along linear bands following geodetic curves between the pores. *Holotype: 3–11.9–41.6.*

These grains are common in the oil shales, and are among the most conspicuous elements found, hence their specific name. They conform in all respects to those of living species of *Alnus*. In size they show a greater range of variation than I have encountered in the pollen of a single living species, consequently it is likely that more than one natural species is involved, but they are well within the size limits of the genus.

The presence of the connecting bands, when these are in evidence, makes the recognition of these grains easy and their identification with the genus *Alnus* certain. Similar bands, it is true, occur in the grains of *Planera*, but these grains are entirely different in other respects. Without the bands the grains of *Alnus* could scarcely be distinguished from those of some species of *Myriophyllum*, *Pterocarya*, and of *Carpinus Betula;* consequently grains of *Alnus* in which the bands are not in evidence, as is

sometimes the case, might confuse the identification of these latter species in any but perfectly preserved specimens.

Alnus pollen grains with both 4 and 5 pores, apparently identical in all respects with those described above have been reported by Kirchheimer (24, 25) from European brown coals. Also grains with 4–6 pores have been reported by the same author but these are of a considerably smaller size and are, therefore, of a different species but the connecting bands between the pores are quite distinct, Kirchheimer points out that, though these grains are smaller than any of *Alnus* with which he has compared them, they are found in association with numerous fossil leaves and flowers which have been identified as *Alnus gracilis* Ung., *A. Kefersteini* Göpp., *A. nostratum* Ung., which is strong evidence that they are truly alder grains. Moreover these small grains of Kirshheimer's appear to be the same as *Alni-pollenites verus* Pot. described by Potonié (41) from Miocene brown coal of Germany. Potonié (38) also describes, under the name of *Pollenites coryphaeus tetraexitum*, grains from Miocene brown coal which correspond to the present species but do not show the connecting bands.

No species of alder have yet been described from the Green River formation but the alders have left their records in most of the larger Tertiary deposits. They occur in the cold Siberian Tertiary (33). In the Tertiary of B. C. they are represented by three species (8). In the Florissant they are represented by two species (26). In the Miocene Latah formation (9) they are represented by two species, including a staminate-catkin and a pistillate cone (29), and in the Denver by two species (31). So it is not surprising that alder pollen is found in the Green River shales and one can predict with certainty that other parts of the plant will be found as the shales are more extensively studied.

Betula claripites sp. nov. (fig. 41). Apparently spheroidal or oblately flattened in life. 22.8–29.6μ in diameter; pores three, protruding owing to the thickening of the exine surrounding them, pore pattern corresponding to the *Betula* type (fig. 36), apertures approximately circular; aspides faintly visible; texture smooth. *Holotype: 4–8.8–65.1.*

These grains match perfectly those of living species of *Betula*, coming perhaps closest to *B. lenta*, and are not likely to be confused with any other member of the family. Only two grains were found which certainly belong to this species and a third, imperfectly preserved, which probably does. Their rounded shape and sharply protruding pores make them rather conspicuous objects, and it is to this fact that the specific name refers, but they are much less abundant than the pollen of *Carpinus* or *Alnus*.

The leaf of a single species of birch (*Betula eocenica* R. W. Brn.) has

been recorded from the Green River formation (17), but, unless a staminate cone bearing recognizable grains is found, it is unsafe to assume that the pollen is of the same species. Similar grains but somewhat smaller, so undoubtedly of another species, have been described from Tertiary brown coals (24).

Betula has a wide distribution in Tertiary formations. It is found in the cold Siberian Tertiary (33), and in most of the principal Tertiary floras of America except those of the southeast regions which were too warm (6).

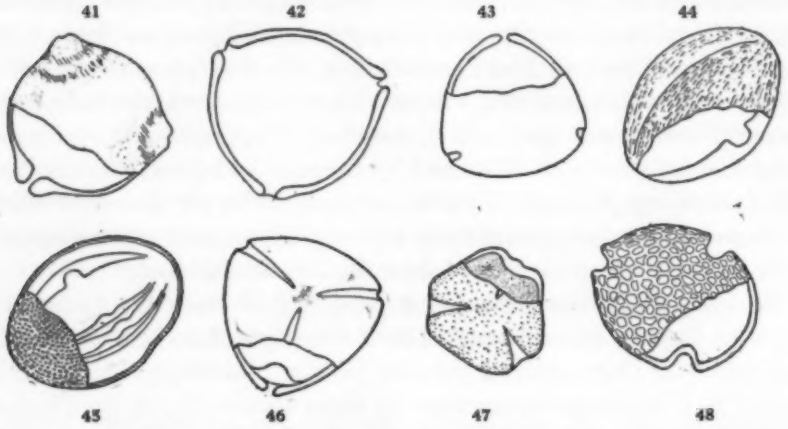


Fig. 41, *Betula claripites*, polar view, drawn as if a part were removed, to show its appearance in optical section; fig. 42, *Carpinus ancipites*, optical section, polar view; fig. 43, *Momipites coryloides*, polar view drawn as if a part were removed, to show its appearance in optical section; fig. 44, *Ailanthipites Berryi*. Side view, drawn as if a part were cut away, to show the inwardly projecting rims of the furrow and germ pore; fig. 45, *Rhoipites Bradleyi*, side view, in optical section except a small part at the upper end which is shown in surface view; fig. 46, *Talisiipites Fischeri*, polar view showing a small part of one side in optical section; fig. 47, *Vitipites dubius*, polar view of surface, a small part on one side shown in optical section; fig. 48, *Tilia crassipites*, polar view of surface on the left and optical section on right.

It is represented in the Florissant (26), in the Latah Miocene (9, 29), in the tertiary of B. C. (8), and in the Denver and associated formations (27). The presence of *Betula* and *Alnus* in the Green River flora suggest a rather cool and humid climate.

Carpinus ancipites sp. nov. (fig. 42). In life apparently oblately flattened angular in outline, 27.4–44.5μ in diameter. Pores 3 or 4, their apertures elliptical; when three, meridionally arranged; when four, on the equator with their major axes converging in pairs; very slightly or not at all protruding, and the exine surrounding them scarcely or not at all thickened; pore pattern as in the *Carpinus* type (fig. 39). Texture smooth. *Holotype: 4–19.1–72.1.*

These grains match exactly the two species of *Carpinus* which I have examined, but in size they have a greater range of variation. They are rather numerous in the shales, but much less so than *Momipites* which they resemble closely. The specific name is derived from Lat. *anceps*, ambiguous, on account of the difficulty of distinguishing them from this latter species.

Carpinus has not hitherto been recorded from the Green River formation, though it was much more abundant, both in species and individuals, during Tertiary times than it is at present, and it is represented in most of the principal Tertiary floras of America except those of the southwest of which the climate was too warm for the Betulaceae.

ULMACEAE

Momipites gen. nov.

Grains spheroidal or oblately flattened and somewhat triangular in outline. Pores three on the equator with their apertures broadly elliptical and meridionally oriented, only slightly protruding above the surface, and with the exine immediately surrounding them slightly thickened, corresponding to the *Corylus* pattern (fig. 38). Texture smooth.

Momipites coryloides sp. nov. (fig. 43). Oblately flattened and triangular in outline, 21–33.1μ in diameter. *Holotype: 5–10.9–52.7.*

These grains are numerous in the oil shales and many of them are so perfectly preserved that the outlines of the subexineous thickenings which surrounded their germ pores in life can be clearly seen. Nevertheless their identification with *Momisia* is not entirely certain for they are scarcely distinguishable from the grains of *Corylus*. They likewise match *Engelhardtia spicata* in all respects except their larger size. But by actual comparison they seem to match most closely the grains of *Momisia*, especially *M. iguanacea*, accordingly they are tentatively referred to this genus.

Neither *Momisia*, *Engelhardtia*, nor *Corylus* have been recorded from the Green River formation, but all three are common genera of North American Tertiary deposits. *Engelhardtia* occurs in the Jackson, Wilcox and Florissant floras, which latter is in part probably a Miocene derivative of the Eocene Green River flora. *Corylus* is known to occur in the Tertiary of British Columbia (8). *Momisia* occurs in the Clairborne and Jackson floras (6). Though *Momisia* has not been recorded as such from the Green River formation, *Celtis debequensis* R. W. Brn. has, and since *Momisia* is regarded by many botanists as a section of the genus *Celtis*, I feel that there is at least a possibility that the pollen, here designated as *Momipites coryloides*, may be that of *Celtis debequensis*.

It is unfortunate that the identification of this pollen cannot be determined with greater certainty because, occurring in the enormous quantity

that it does in the oil shales, it must have come from one of the dominant members of the Green River flora. If it turns out to belong to *Momisia* or *Engelhardtia* it points to southern connections of the Green River flora, but if it turns out to belong to *Corylus* it points to the northern connection of this flora.

Similar pollen grains are described from Eocene brown coal of Germany by Kirchheimer (24). He suggests that such a form might belong to some member of the Betulaceae, especially *Corylus*, but, he states, it is also closely approached by the grains of *Ostrya* and *Myrica*. I do not feel that there is any danger of confusing the present species from the Green River formation with either of these two latter genera.

SIMARUBACEAE

Ailanthipites gen. nov.

Generally ellipsoidal, but somewhat various in shape according to the degree of their expansion, tricolpate with furrows long, reaching almost from pole to pole, furrow rim and pore rim conspicuous, projecting deeply inward. Exine reticulate-pitted with the pits elongate and linearly arranged forming a sort of thumb-print pattern.

Ailanthipites Berryi sp. nov. (fig. 44). Grains 20–25.1μ broad and 26–30μ long. *Holotype: 36-19.8-61.5.*

These grains match perfectly those of *Ailanthus glandulosa*, and it is with a fair degree of confidence that they are assigned to that genus. The only other form of grain I know which they resemble is that of *Spondias Mombin* (46), but the grains of the latter are much larger—34–39μ broad and 43–50μ long—which makes it extremely unlikely that these fossils belong to that genus. They are obviously insect borne yet they occur in the shales in large numbers. Therefore, they belong to a plant which grew abundantly near the place of deposition.

Ailanthus is represented in the Green River flora by the fossil species *A. longi-petiolata* Lesquereux. There is, therefore, at least a possibility that these grains belong to that species. "The Chinese tree of heaven (*Ailanthus*) is found fossil in the late Miocene lake beds at Florissant, Colorado and at other places and times in North America, but has not been native for hundreds of thousands of years, yet it has become effectively naturalized in the last few centuries since it was introduced by man." The specific name is given in honor of Edward W. Berry from whose work the quotation is taken, and who has contributed perhaps more than any other single investigator to our knowledge of Tertiary floras.

ANACARDIACEAE

Rhoipites gen. nov.

Ellipsoidal, tricolpate, with furrows long and pointed. Furrow and pore thickenings conspicuous, projecting deeply inwards. Exine rather finely reticulate-pitted.

Rhoipites Bradleyi sp. nov. (fig. 45). Grains 25×35μ. *Holotype: 36–19.6–61.8. At this reading are four grains of this species. The holotype is the one illustrated.*

This species matches perfectly with the grain of *Rhus typhina*. It is, however, of a generalized type which makes the evidence of matching alone, somewhat uncertain. It is rather abundant in the shales, and since it has the appearance of being primarily insect pollinated the plant which produced it must have lived in great abundance and close to the place of deposition.

Rhus is represented in the Green River flora by five species, and from the same family have been recorded one species of *Schmaltzia* and one of *Anacardites*. *Rhus* is also known from the Raton (36), Animas (28) and Latah (9, 29) formations. Consequently the finding of *Rhus* pollen in the Green River oil shales is to be expected. The specific name of the present species is given in honor of W. H. Bradley in recognition of his studies of the Green River formation.

SAPINDACEAE

Talisiipites gen. nov.

Oblately flattened, triangular in polar view, tricolpate, with furrows long, narrow and shallow, each enclosing a small germ pore. Pores aspidate, surrounded by a subexineous thickening similar to those of the grains of the Betulaceae. Exine thin and rather finely granular, more evidently so near the pores.

Talisiipites Fischeri sp. nov. (fig. 46). Grains 28.5μ in diameter. *Holotype: 3–10–44.5.*

These grains are rather common, four were examined in detail. They match perfectly *Talisia depressa* (46). Since this is rather a unique type in its combination of aspidate pores with long tapering furrows, one that I have not encountered elsewhere, it is with a fair degree of confidence that it is assigned to the genus *Talisia*. The specific name of these grains is given in honor of Hugo Fischer whose inaugural dissertation, dated Breslau 1890, has become a classic in pollen literature.

A species of this family, *Thouinia* (*Talisia*) *eocenica* R. W. Brn., is

represented in the Green River formation and it is indeed possible that the grains described here belong to that species. What appears to be the same species is described by Potonié (40) as *Pollenites vestibulum* from Eocene brown coal of Germany.

VITACEAE

Vitipites gen. nov.

Oblately flattened, hexagonal in polar view, rather small, tricolpate with furrows sharply defined, long and tapering. Exine finely and faintly pitted.

Vitipites dubius sp. nov. (fig. 47). Grains about 22.8μ broad. *Holotype: 4–8.5–66.3.*

A single specimen of this species was found. It matches exactly with the pollen grain of *Vitis vinifera*. Nevertheless since it is of a rather generalized type its identification with the genus *Vitis* is not entirely certain.

Vitis has not hitherto been recorded from the Green River formation, but is known to occur in its derivative flora, the Miocene Florissant. It has also been recorded from the Denver, Vermejo and Raton formations (31) so it is to be expected in that of the Green River. An allied species, *Parthenocissus tertiaria* (Lesquereux) Knowlton has been recorded from this formation (27), but the pollen grains of the living species of these two genera are quite distinct and not likely to be confused.

TILIACEAE

Tilia

Grains of the living species, *T. americana*, are lens-shaped, 35.3–37.6μ in diameter, always with three germ pores arranged around the equator and deeply sunken in very short pit-like germinal furrows, with exine rather thick and finely reticulate-pitted.

Among the present fossil material are found four distinct forms which answer more or less closely to this description.

The other members of the Tiliaceae, *Triumfetta* and *Grewia*, which are believed to have been widely represented in Eocene time, have pollen grains entirely different. Those of both *Triumfetta* and *Grewia* are ellipsoidal, 43–54μ long and about 2/3 as broad, with long tapering furrows reaching almost from pole to pole, and with coarsely reticulate exine. I did not find them represented in the oil shales, nor is there any possibility that any of the fossil material here included under *Tilia* can belong to either of these genera.

Tilia has not hitherto been recorded from the Green River formation, and the family is, up to the present, represented in that formation only by

a single species of *Grewiopsis*. But *Tilia* was rather wide spread in the Tertiary period. It is recorded from the Eocene Jackson and Raton floras (36) and from the Miocene Latah (9) and Florissant (18, 26) floras, so it is to be expected in that of the Green River.

Two species of *Tilia* pollen, *Tiliae-pollenites instructus* Pot., and *T.-p. indubitabilis* Pot. which may be the same as *T. crassipites* among the following, have been described from the European brown coals by Potonié (39), but he states that they are granular whereas the following are reticu-

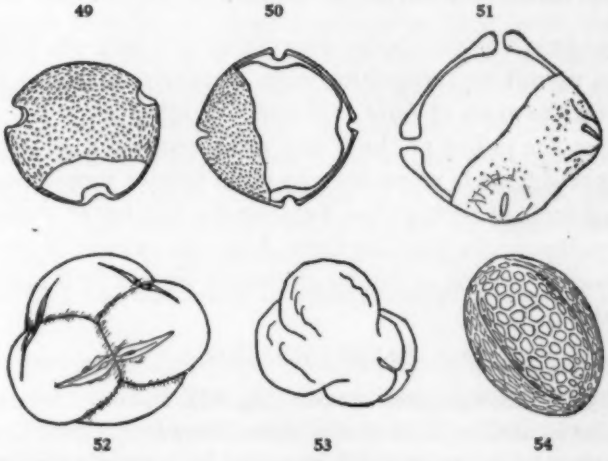


Fig. 49, *Tilia vescipites*, polar view of surface, but with a small part shown in optical section; fig. 50, *Tilia tetraforaminipites*, polar view, the left of the figure in optical section, the right in surface view; fig. 51, *Myriophyllum ambiguipites*, polar view shown partly in optical section and partly in surface view; fig. 52, *Ericipites longisulcatus*, a tetrad of united grains; fig. 53, *Ericipites brevisulcatus*, a tetrad of united grains; fig. 54, *Caprifoliipites viridi-fluminis*, side view.

late-pitted as are those of the living *T. americana*. Kirchheimer (24), also describes and illustrates a species of *Tilia* pollen from the Tertiary brown coal of Germany, but it is apparently not the same as any of those described below for it is 31.2–40.3μ in diameter and is stated to be granular.

Tilia crassipites sp. nov. (fig. 48). Grains apparently lens-shaped or at least somewhat oblately flattened in life, though the present specimen is completely flattened in the plane of the section and somewhat distorted, 43.3 $\times$36.5μ. Pores three, sunken in deep pits. Exine thick and coarsely reticulate. *Holotype: 4–8.6–65.2.*

This fossil bears a marked resemblance to the grain of *Tilia americana* but differs in its larger size and more coarsely reticulate surface. It is to this character that the specific name refers.

Tilia vescipites sp. nov. (fig. 49). Similar to the preceding, but 27.4μ in diameter and with exine finely reticulate-pitted. It is to the fineness of the texture that the specific name refers. *Holotype: 5–10.8–48.9.*

This fossil matches exactly the grain of *T. americana* except for its size which is about 10μ in diameter less.

Tilia tetraforaminipites sp. nov. (fig. 50). Similar to the preceding, except that the exine is more finely pitted, and there are four instead of three pores, 28.5μ in diameter. *Holotype: 6—16.1–62.4.*

Three specimens of this species were found but only one is well enough preserved to permit its recognition with certainty. This species matches almost exactly the grain of *Tilia americana*, except in its possession of four pores. Though the pollen of the living *Tilia americana* appears to be always three pored, that is no reason why other species should not have four pores in all or some of their grains, because the number of germ pores possessed by a pollen grain, whether three, four, six or even higher numbers, may be a specific, generic or family character, or merely a matter of individual variation.

HALORAGIDACEAE

Myriophyllum ambiguipites sp. nov. (fig. 51). Oblately flattened and decidedly angular in outline 21.6μ in diameter. Pores four, abruptly protruding above the surface of the grain and surrounded by a greatly thickened ring of the exine, of the *Betula* pore pattern (fig. 36) with apertures slit-shaped and converging in pairs. Exine slightly granular, particularly around the pores. *Holotype: 3—11.9–41.0.*

Only a single specimen of this species was found. It matches exactly with the grains of *Myriophyllum spicatum* L. and I believe that the rather extreme and abrupt thickening of the exine surrounding the pores is distinctive. To some extent this fossil species resembles the grain of *Alnus*, but lacks the connecting bands of the latter. It also resembles the four-pored grains of *Comptonia*, but the germinal apertures of these are never slit-shaped, being instead, circular or broadly elliptical.

Myriophyllum has not been recorded from the Green River formation, nor, so far as I am aware, elsewhere in the Tertiary.

Ericipites gen. nov.

Grains in tetrahedral tetrads, generally tightly appressed. Exine rather thin, smooth or somewhat granular. Furrows of each grain of the tetrad three, of various length in the different species; each contiguous and continuous with one of the furrows of each of its three neighbors across the suture between

their contact faces. Pores three, enclosed by the furrows, those of adjacent furrows close to and facing each other across the suture.

Among the living species of Ericaceae the pollen grains of the majority answer this description. But those of the Clethraceae and Monotropaceae which are frequently, though probably mistakenly, included in the family, are always single. Among the true Ericaceae the grains of many species, as for example those of *Rhododendron*, *Kalmia* and some species of *Erica* are provided with extremely slender 'vicin' threads which cause them to become tangled together in large numbers as they leave their anthers. There is much of a sameness of pollen form throughout most of the family, but such characters as the size of the grains, the length and breadth of the furrows, and the texture of the exine can sometimes be used to distinguish the different genera from each other. Even among living species, however, these distinctions are vague and difficult of interpretation, consequently the present fossil genus is established to receive all fossil pollen which is known to belong to the family Ericaceae, exclusive of the Clethraceae and Monotropaceae, which are in reality almost unrelated to the true Ericaceae.

A single species of Ericaceae, *Andromeda delicatula* Lesquereux has been previously recorded from the Green River formation (27), and the genus is also found represented in the Florissant beds (18) and Raton formation (36), but neither of the two fossil species recorded here match the grains of living species of *Andromeda*. Pollen of several kinds of Ericaceae are recorded from Tertiary brown coals of Europe (24, 41).

Ericipites longisulcatus sp. nov. (fig. 52). Tetrads 36–45.6μ broad. Exine mostly smooth but faintly roughened in some regions. Furrows long and slender, tapering to their distal ends; the presence of pores enclosed by each is indicated by a slight bulge near its proximal end. *Holotype: 4–19.8–70.1.*

Only two specimens of this species were found, and they are in actual contact with each other. The faintly granular appearance of some parts of the exine suggests that in life these grains were granular throughout, as are those of most living Ericaceae. No vicin threads were observed, but the fact that the only two specimens that were found are in contact with each other is strong evidence that they arrived at their place of entombment tangled together by such threads. In the grains of *Andromeda*, the only member of the Ericaceae so far recorded from the Green River formation, such threads are lacking; furthermore the furrows of the grains of *Andromeda* are much broader and shorter than those of the present fossil species, consequently it cannot be *Andromeda*. In this and other characters

the present fossil species resembles more closely the grains of some species of *Erica*.

Ericipites brevisulcatus sp. nov. (fig. 53). Tetrads 45.6μ broad. Exine smooth. Furrows short. *Holotype: 8-5.5-62.8.*

A single specimen of this species was found, and it is in so poor a state of preservation that no details further than its general resemblance to the Ericaceae could be seen. As far as these observations go it corresponds with *Calluna vulgaris* Salisb.

CAPRIFOLIACEAE

Caprifoliipites gen. nov.

Grains very small, among the smallest found in the oil shales, ellipsoidal, tricolpate with furrows long and pointed, with conspicuous internally projecting furrow rims and pore rims. Exine coarsely reticulate.

Caprifoliipites viridi-fluminis sp. nov. (fig. 54). Grains 11.4–17.1μ broad and 16.5–22.8μ long. *Holotype: 36-7.3-60.7.*

These beautiful little grains are among the most abundant species in the shales, and since they are nearly always perfectly preserved they form one of the most conspicuous and characteristic elements of the shales, hence their specific name. In form they match almost perfectly with the grains of *Viburnum*, but in their small size they compare more favorably with the very similar grains of *Sambucus*. Unfortunately, however, these fossil grains represent a generalized type, so that their assignment to the Caprifoliaceae is little more than a guess, though I believe it has a fair degree of probability.

The Caprifoliaceae are not represented in the Green River flora but are found in the Miocene Florissant of Colorado. *Viburnum* was an exceedingly widespread and characteristic genus of Tertiary times occurring in the Vermejo, Raton, Denver, Animas, Wilcox and Latah formations, so it is to be expected in the Green River flora.

SUMMARY AND CONCLUSIONS

From the oil shales of the Eocene Green River have been described forty-three species of fossil pollen, in thirty-four genera. All, except one, are assignable to living genera or families. One species is an abietineous grain belonging to an extinct genus. There still remain in the material examined possibly twice as many more pollen species awaiting identification.

The list of families and genera of plants that have been found to be represented in this material by pollen is shown in Table I. Of these, twenty-

nine species (21 genera) are new to the Green River flora, while only eighteen species, in thirteen genera, are of genera already represented in the Green River flora. This disagreement between the fossil pollen record and the fossil record of other parts of plants, is apparently due, in part at least, to the greater mobility of pollen. Twenty-nine of the pollen species were probably wind borne, and most of these are of plants which do not grow in or near water, so had little chance, except through their pollen, of ever being represented in the oil shales, which were laid down in water. A further study of the unidentified pollen in the material is likely to only increase this disagreement, because the examination of the material was prefaced by a study of the pollen of the living representatives of the Green River flora, making their recognition fairly certain if encountered.

On the whole the flora, as indicated by the pollen record, was decidedly less tropical in nature than that already recorded from the Green River formation. This appears to have been due to the fact that the two records are not entirely contemporaneous. In a private communication upon this subject Dr. Bradley states, "On the basis of the varves or annual layers in certain beds of the Green River formation, I have estimated that the leaf-bearing horizons were deposited at least one million years later than most of the pollen-bearing oil shales which you have been studying. The basis for estimating this time interval is given in another paper of mine, Professional Paper 158, in which I also discuss some aspects of the Green River climate. According to this estimate the time interval between the pollen beds and the greater part of the known Green River flora is amply long for a rather distinct climatic change. In as much as some of the lowermost beds in the Green River formation also contain a flora which is nearly if not quite identical with that obtained from the uppermost beds, it seems that the oil shale was formed during low stages of the lake under considerably drier conditions than those prevailing either during the lower part of the Green River epoch or during the latest phases of it. This idea is further strengthened by the fact that salt crystal molds are commonly associated with the oil shale beds."

That the pollen beds were deposited during a period of extreme aridity is confirmed by the finding of the pollen of *Ephedra* which is a desert plant. Nevertheless the bulk of the pollen at exactly the same level was contributed by trees of a forest type similar to that of the northern and middle Atlantic states of the present time, demanding conditions entirely different from those congenial to *Ephedra*.

With such evidences at hand one can hardly refrain from hazarding a reconstruction of the ancient Green River lake and the conditions surrounding it. The lake must have lain in a hot desert valley, and have

been fed by streams flowing into it from regions where there was heavier rainfall. The lake was shallow and muddy, possibly consisting of a succession of small ponds, as suggested by Brown (17), for in the water grew pondweeds (*Potamogeton*), water milfoils (*Myriophyllum*), and along its margins arrow arum (*Peltandra*). Immediately surrounding the lake must have been extensive marshy areas in which grew cypress (*Taxodium*), the water pine (*Glyptostrobus*), some heaths, and quantities of willows (*Salix*), and in less marshy regions a few palms and cycads amid the usual underbrush, including such shrubs as the marsh elders or possibly viburnums, and sumacs, and the usual tangle of vines as the wild grapes (*Vitis*) and cat-briars (*Smilax*). Here also grew *Myrica*. Its pollen is of such a character that it could have been carried from the hills several miles away, but the presence of eight species already recorded by abundant material of leaves and stems in the shales, suggests that the pollen came from species which grew in or near the water.

All of these and the numerous other plants whose substance went to make up the beds must have derived their moisture from the lake itself, for the presence of *Ephedra* pollen in the shales indicates that the region was surrounded by arid conditions not very far away, just as certainly as the presence of salt crystal molds indicates that from time to time the lake partly dried up. But the mountains surrounding the lake must have been well watered, a condition which prevails in much of the arid regions of the southwestern part of the United States today. At the higher altitudes flourished a mesophytic forest, dominated by pines, firs, spruces, with a sprinkling of hemlock, possibly *Cedrus* and one or more species of conifer unknown to us. That this rich coniferous forest flourished a long way from the lake is attested by the fact that it has hitherto only been represented in the lacustrine deposits by a single winged seed and a small twig. Intermingled with these, but in considerably lesser numbers, were hickories, walnuts and *Engelhardtia*, with birches and basswood barely able to maintain a foothold, and here and there a tulip tree or magnolia. Leading down from these well watered mountains were small canyons in which grew thickets of alder and ironwood (*Carpinus*). That these did not grow near the lake itself is suggested by the absence, so far discovered, of their leaves etc. in the shales.

Something should be said of the pollen which was not found, though, of course, anything said on this score may be contradicted by further studies. Herbaceous plants, apart from a few aquatics are not represented. And among the aquatics, *Typha* and *Sparganium* were not found. Had these plants existed their pollen would very likely have been found for it is produced in large quantities and is of such a character that it is not likely

to be overlooked. Grasses are not represented but this may have been due to the inability of their pollen to be preserved in the shales in recognizable form, though it has frequently been recorded from Post-pleistocene deposits. The salt bushes (*Atriplex*), a genus of wind pollinated plants, abundant in the region at the present time, are not represented by pollen in the shales, nor are any other members of the Chenopodiaceae to which they belong, nor the allied family, Amaranthaceae. But the most significant of all is the entire absence of the great herbaceous family Compositae. Their pollen is among the most easily recognized, and is of such a character that it could scarcely have failed to be preserved, if present. The pollen of the entomophilous members of the group, it is true, might never have reached the lake, but it is scarcely possible that the anemophilous ragweeds or their allies could have flourished within miles of the lake and not have left their record in the shales by their pollen. Nor do we find represented the great anemophilous genus of the Compositae, the sagebrushes, which are abundant throughout the region at the present time. Both of these groups, in at least some of their species, delight in the conditions under which *Ephedra* flourishes, and if they had been present their pollen would have had a much better chance than that of *Ephedra* of reaching the lake, owing to the smaller size of their grains and more prolific production. Therefore we are forced to concludethat neither the ragweeds and their allies, nor the sagebrushes were represented in the flora of the Green River Epoch. In this connection it should be remembered that the Green River formation was laid down early in the Eocene period. Therefore the absence from it of terrestrial herbs is entirely in keeping with the thesis put forward by E.W. Sinnott, that the herbaceous type was developed in temperate regions during Eocene time in response to a progressive refrigeration. At this period terrestrial types were only beginning to be developed.

In closing I wish to thank Dr. E. D. Merrill and the staff of the New York Botanical Garden for the use of the herbarium, without which many of the identifications achieved would have been impossible. I am also indebted to Dr. E. W. Berry for much of the literature on Tertiary floras and for valuable suggestions. But especially am I indebted to the late Dr. Arthur Hollick with whom discussions of the various Tertiary floras were a frequent source of inspiration and encouragement.

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TABLE 1[a]

List of families and genera represented in the Green River oil shales

	NUMBER OF SPECIES	IDENTIFICATION SOMEWHAT DOUBTFUL (X)	NUMBER OF SPECIES ALREADY KNOWN IN GREEN RIVER FLORA	POLLINATION BY WIND (W) BY INSECT (I)		NUMBER OF SPECIES	IDENTIFICATION SOMEWHAT DOUBTFUL	NUMBER OF SPECIES ALREADY KNOWN IN GREEN RIVER FLORA	POLLINATION BY WIND (W) BY INSECT (I)
Cycadaceae					Myricaceae				
Cycas	1		0	W?	Myrica	1		8	W
Dioon	1	x	0	W?	Salicaceae				
Coniferae					Salix	1		4	W-I
Abietineae					Betulaceae				
Pinus	3		1	W	Alnus	1		0	W
Picea	1		1	W	Betula	1		1	W
Abies	1		0	W	Carpinus	1		0	W
Cedrus	1	x	0	W	Ulmaceae				
(Abietipites)	1		0	W	Momisia	1	x	0	W
Tsuga	1		0	W	Simarubaceae				
Taxodineae					Ailanthus	1	x	1	I
Taxodium	1		0	W	Anacardiacea				
Glyptostrobus	1		0	W	Rhus	1	x	5	I
Cunninghamia	1		0	W	Sapindaceae				
Gnetaceae					Talisia	1	x	1	?
Ephedra	1		0	W	Vitaceae				
Najadaceae					Vitis	1	x	0	I
Potamogeton	1		0	I?	Tiliaceae				
Arecaceae					Tilia	3		0	W-I
(Arecipites)	2	x	4	W?	Haloragidaceae				
Araceae					Myriophyllum	1		0	I?
Peltandra	1	x	0	I	Ericaceae				
Liliaceae					(Ericipites)	2		1	I
Smilax	3	x	0	I	Caprifoliaceae				
Magnoliaceae					Sambucus	1	x	1	I
Liriodendron	1		0	I					
Juglandaceae									
Hicoria	2		1	W					
Juglans	1		5	W					
Engelhardtia	1		0	W					

[a] This list should be compared with the list of the families and genera of the known Green River flora, compiled from Knowlton and Brown, and which has been published in the first article of the present series (46).

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INDEX TO AMERICAN BOTANICAL LITERATURE
1931–1933

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